

The Hawaiian amphibious caterpillar guild: new species of *Hyposmocoma* (Lepidoptera: Cosmopterigidae) confirm distinct aquatic invasions and complex speciation patterns

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Although aquatic caterpillars are a globally rare lifestyle, we have found them in multiple, independent lineages of the endemic moth genus *Hyposmocoma* across all of the Hawaiian Islands with flowing water. We formally describe 11 new species of *Hyposmocoma* that belong to four different larval case types: cone, bugle, medium burrito, and large burrito: *Hyposmocoma kahamanoa* sp. nov. from Oahu Island, *Hyposmocoma kamakou* sp. nov. from Molokai Island, *Hyposmocoma kahaiao* sp. nov., *Hyposmocoma waihohonu* sp. nov., and *Hyposmocoma moopalikea* sp. nov. from Maui Island, and *Hyposmocoma aumakuawai* sp. nov., *Hyposmocoma eepawai* sp. nov., *Hyposmocoma ipowainui* sp. nov., *Hyposmocoma kawaikoi* sp. nov., *Hyposmocoma uhauiole* sp. nov., and *Hyposmocoma wailua* sp. nov. from Kauai Island. We also illustrate and describe in detail the aquatic case-bearing larva of *Hyposmocoma kahamanoa*. Despite having similar ecologies as algae and lichen grazers at and below the water line of streams, prior research indicates that species with each case type constitute an independent lineage, with terrestrial sister taxa, and therefore the different groups of species bearing unique case types each represent an independent aquatic invasion. The case-bearing larvae often occur sympatrically, and on Kauai even species with similar case-types occur together, suggesting complex patterns of speciation and either past periods of isolation or sympatric speciation. Phylogenetic analysis of 2243 base pairs from two nuclear and one mitochondrial gene for 18 species confirm that each species is endemic to a single volcano, and that morphological divergence within case-types has not been dramatic. Diversification has been complex, and superficially similar case type lineages are not all monophyletic. Kauai, the oldest but smallest of the major high islands, supports more species in the aquatic guild than any other island, thus island age, rather than size, may be important in generating diversity in this group.

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INTRODUCTION

Aquatic Lepidoptera are a globally rare phenomenon. Of the approximately 150 000 described species of Lepidoptera worldwide (Heppner, 1991) only an

estimated 760 (0.5%) are considered truly aquatic (Mey & Speidel, 2008), having one or all stages morphologically adapted to an underwater lifestyle. Aquatic species occur primarily in the subfamily Acentropinae (Lepidoptera: Crambidae), formerly known as Nymphulinae, perhaps the most diverse and studied subfamily of aquatic moths (Munroe & Solis, 1998; Speidel, 2005). The strategies employed by larvae encompass various methods of respiration

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in water (Resh *et al.*, 2008), from air-breathers involving plastron-like layers of air, oxygen within cases, or obtaining air from the interstitial space of the host plant, to breathing dissolved oxygen through tracheal gills, a unique trait in Lepidoptera (Welsh, 1922; Munroe & Solis, 1998; Speidel, 2005; Solis, 2008).

Recently, we discovered species of aquatic moths across the Hawaiian archipelago (Rubinoff, 2008; Rubinoff & Schmitz, 2010), all of which are members of the endemic case-bearing moth genus *Hypsmocoma* (Lepidoptera: Cosmopterigidae), which represents a megadiverse and spectacular insular radiation with over 350 species (Zimmerman, 1978). Although some *Hypsmocoma* species were associated with case-making larvae by previous researchers, the aquatic species and their remarkable lifestyle inexplicably remained unrecorded and unpublished (Walsingham, 1907; Lange, 1978; Zimmerman, 1978), despite such a conspicuous and unusual ecology. The caterpillars recently identified as aquatic (Rubinoff & Schmitz, 2010) live inside portable cases in fast-moving mountain streams on various islands. As these streams usually drain rainforest mountaintops, they are subject to sudden increases in flow, and dramatic, frequent, scouring events. The larvae have adapted to the extremely treacherous and variable conditions occurring there by air-breathing during dry periods and breathing underwater when submerged by floods or when diving to feed on submerged algae or lichen. They are further adapted to the stream environment by using silk to secure themselves on rocks as they crawl on submerged substrates to avoid being washed out to the sea during flood events (Rubinoff, 2008; Rubinoff & Schmitz, 2010). The cases are made by incorporating large numbers of tiny sand grains, bits of algae, lichens, and, in some cases, diatoms in a silk matrix that is closed by a remarkable operculum (trap door or lid) adorned with stone weights that can be closed tightly from the inside by the larva with the aid of the mandibles (Zimmerman, 1978). The larvae can be abundant on rocks covered with lichen and mosses (Zimmerman, 1978), and cases containing larvae can be found on rocks throughout open areas of streams at or below the water surface feeding on lichens and algae (Rubinoff, 2008).

Recent molecular research shows that the radiation of cone-cased aquatic *Hypsmocoma* gave rise to a single endemic species on each of the main islands of Oahu, Molokai, and Maui, but to three species endemic to Kauai, demonstrating inter- but also intra-island speciation in these remarkable moths (Rubinoff, 2008). In their habitat, these caterpillars, with their distinctive thorn-like case and prominent thoracic legs, bear great resemblance to the larvae of Trichoptera, of which there are no endemic species in

Hawaii (Zimmerman, 1947, 1978). Despite single-island endemic aquatic species having been collected on four different main Hawaiian Islands, only *Hypsmocoma saccophora*, a cone-case terrestrial species, was previously described from reared adults. *Hypsmocoma saccophora* is endemic to the Waianae Mountains of western Oahu Island (Walsingham, 1907), and its terrestrial ecology, we now know, is unusual in the cone-cased lineage, which is dominated by until now undescribed aquatic species (Rubinoff, 2008). The fact that only *H. saccophora* was found and recognized by previous workers raises some questions about collecting bias or methods during historical research efforts. Our investigations demonstrated that an aquatic lifestyle evolve not only in the cone-bearing larvae, but also independently in other lineages of *Hypsmocoma* (Rubinoff & Schmitz, 2010). In this work, we describe 11 new species of aquatic case-bearing *Hypsmocoma* moths not only from the cone-cased group (Rubinoff, 2008) but also three other lineages (bugle, medium burrito, and large burrito), with special emphasis on the fine morphology of cone case-bearing larva. We also present a molecular phylogeny based on three genes [cytochrome oxidase I (*COI*), elongation factor 1 alpha (*EF1α*), and carbamoylphosphate synthetase (*CAD*)] including 38 individuals from 18 species across *Hypsmocoma* and two outgroups to demonstrate the systematic placement and relationships of the newly described species and to elucidate the parallel evolution of aquatic ecology.

MATERIAL AND METHODS

SAMPLING AND REARING

The specimens forming the basis of this study were reared from case-making larvae collected in the field as part of a broader study of the genus. We also collected large numbers of larvae from a range of species in a variety of other habitats, including forest, scrub, and seashore, but only encountered aquatic species near and in streams. We brought the larvae into the lab and separated them by collecting location and case type in Petri dishes. Larvae were offered carrot, lichen, and commercial fish food (TetraMin). For each field-collected larva, a unique data log entry (e.g. #DR08D4) was assigned, which includes date and location of capture, digital picture of larva, record of larval behaviour, date of adult moth emergence, and digital picture of adult moth. Adults of many, but not all, *Hypsmocoma* species, including the aquatic taxa considered here, are apparently not strongly attracted to light. Hence, few adults were collected even when a UV-light trap was placed along a stream where adults were observed earlier the same day. While collecting larvae we frequently observed adult

moths flying between emergent rocks, crawling, and mating; therefore, many aquatic species may be diurnal.

For holotypes, information is copied precisely from labels with slashes expressing changes of lines and abbreviations spelled out in square brackets. For paratypes, information is recorded without indications of line changes. For each holotype, the data label is printed in black on white card stock: the holotype label is hand-written in black ink on red card stock. The following acronyms are used: BPBM, Bernice Pauahi Bishop Museum, Honolulu, USA; MHNG, Muséum d'histoire naturelle de Genève, Geneva, Switzerland; UHIM, University of Hawaii Insect Museum, Honolulu, USA; and USNM, National Museum of Natural History, Washington, DC, USA.

MORPHOLOGICAL DESCRIPTIONS

Genitalia were dissected after the abdomen had macerated in a cold 20% KOH solution overnight. The dissected parts were kept in lactic acid stained with orange G to enhance contrast of hardened cuticle for descriptive purposes. Genitalia were subsequently stained with chlorazol black to stain membranes, dehydrated in 95% ethyl alcohol, fixed in absolute isopropanol, and mounted on slides in Euparal. The forewing and cases lengths were measured with a reticule on a stereomicroscope. The illustrations of the moths, cases, and genitalia were made with an Olympus QColor3 camera mounted on an Olympus SZX10 stereomicroscope. To enhance the depth of field, images were stacked and reconstructed using the freely available software CombineZM (<http://www.hadleyweb.pwp.blueyonder.co.uk/>).

For the study of specimens using electron microscopy, larvae and cases were fixed in a 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer, washed in 0.1 M cacodylate buffer, postfixed in 1.0% osmium tetroxide in 0.1 M sodium cacodylate buffer, and dehydrated in increasing concentrations of EtOH to absolute EtOH. After dehydration, specimens were critical-point dried using a Tousimis critical point dryer, mounted on stubs, and sputter coated with gold/palladium using a Hummer 6.2 sputter coater. The ultrastructure of the larvae and cases was studied with a Hitachi S-800 field emission scanning electron microscope.

Gross morphological observations and measurements of the larvae were made using a LEITZ dissecting microscope (reflected light) with a calibrated micrometer. Maps of the larval chaetotaxy were initially drawn using a WILD compound microscope with a camera lucida attachment. Terminology for chaetotaxy follows Stehr (1987).

MOLECULAR AND PHYLOGENETIC ANALYSES

DNA extraction was performed for two specimens of each aquatic *Hyposmocoma* species. Outgroup taxa were selected from the sister genus *Euperissus*. Fragments of the mitochondrial gene *COI* and nuclear genes *EF1 α* and *CAD* were obtained by DNA amplification and sequencing, according to the protocol described in Rubinoff & Schmitz (2010). The phylogenetic tree was inferred using the maximum likelihood (ML) method devised by Felsenstein (1981) and implemented in RAxML 7.0.4 (Stamatakis, Hoover & Rougemont, 2008). The three gene fragments were combined and all model parameters were estimated independently and simultaneously for each gene partition under a general time reversible model (GTR + proportion of invariable site (I) + shape parameter of the gamma distribution (Γ)), executing 1000 rapid bootstrap inferences (Felsenstein, 1981) before a thorough ML search. The phylogenetic analysis was run through the Cipres web portal v.1.15 at the San Diego Supercomputer Center, USA. Outgroups and species chosen for aquatic species analysis were based on results of a much larger dataset including many terrestrial species (Rubinoff & Schmitz, 2010).

EXPERIMENTAL OBSERVATIONS

Laboratory experiments on the ability of the larvae to thrive underwater were carried out by completely immersing rocks covered with algae and cone-case larvae in a 37.84 L commercial aquarium. Next to the algae-covered rocks we placed a commercial aerator for household aquariums in order to recreate the high dissolved oxygen conditions found in the fast-flowing streams. Additionally, we made extensive observations of behaviour during collecting trips to the field over a 6-year period (2003–09). These were entered in the rearing log, and used to understand the caterpillars' ecology.

SYSTEMATICS

HYPSMOCOMA KAHAMANO SCHMITZ & RUBINOFF SP. NOV. (FIGS 1A, 2A, 3–5, 11A)

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Oahu, Palolo stream | 'cone' case, IV-25-20[08] | em[ergence]. V-2-[20]08, #DR08D4 | leg[it]. P[atrick]. Schmitz, W[ill]. Haines'; [2] 'HOLOTYPE | Hyposmocoma | kahamanoa | Schmitz and Rubinoff'. Specimen in good condition. Deposited in the UHIM.

PARATYPES: 24 ♂, 15 ♀, with same data as holotype except date of emergence: 29.iv.2008 (1 ♂), 2.v.2008 (1 ♂), 9.v.2008 (1 ♀), 30.v.2008 (1 ♂, 1 ♀), 9.vi.2008 (2 ♂, one dissected PS168), 12.vi.2008 (3 ♂), 30.vi.2008 (1 ♀), 18.vii.2008 (1 ♂), 20.viii.2008

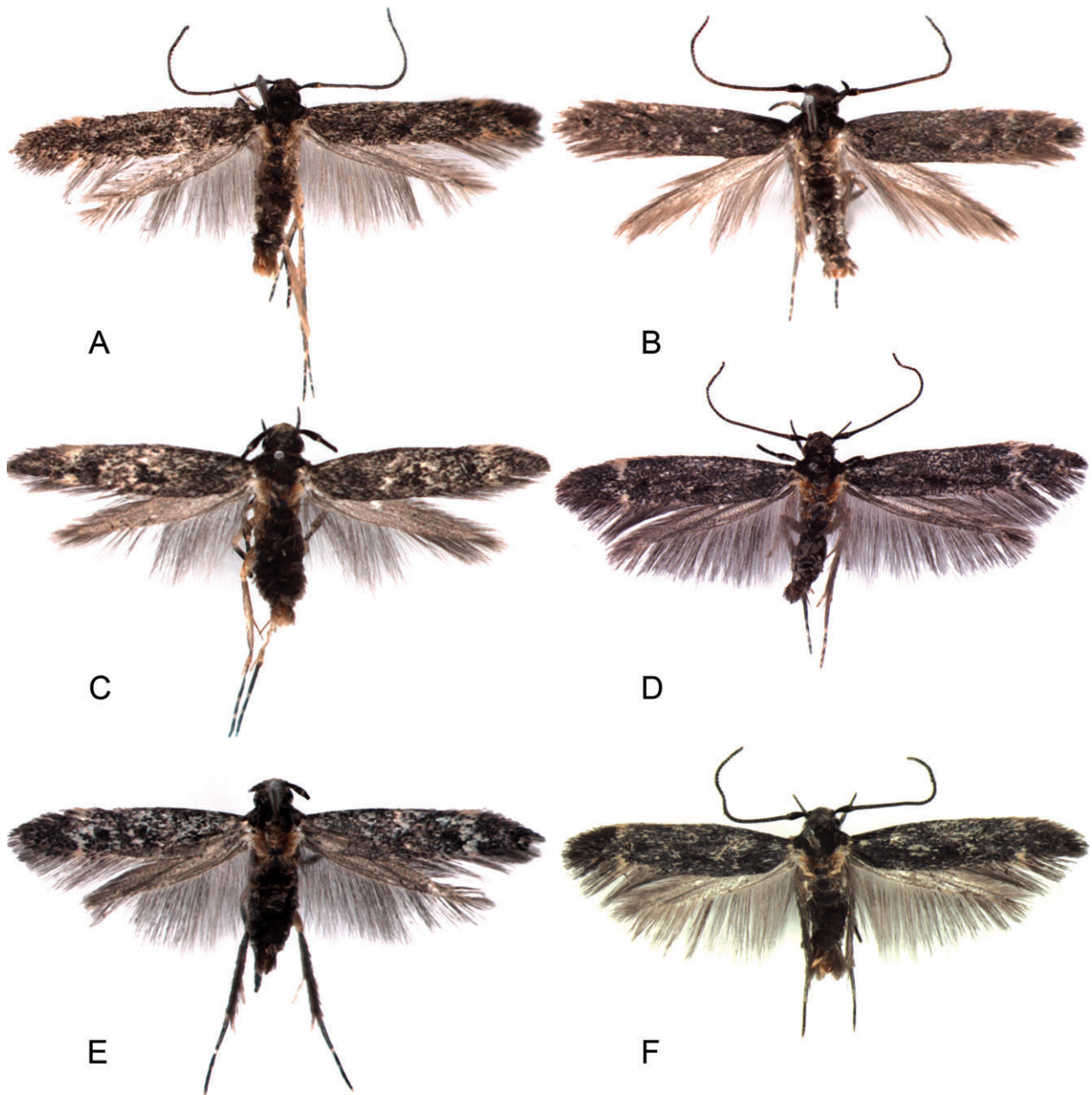


Figure 1. Holotypes of aquatic cone-case *Hypasmocoma* spp., adult males. A, *Hypasmocoma kahamanoa* sp. nov.; B, *Hypasmocoma uhauiole* sp. nov.; C, *Hypasmocoma kahaiao* sp. nov.; D, *Hypasmocoma kawaiikoi* sp. nov.; E, *Hypasmocoma kamakou* sp. nov.; F, *Hypasmocoma wailua* sp. nov.

(1 ♀, #DR08D4, *leg[ita]*. P[atrick]. Schmitz, W[ill]. Haines; 2 ♂, 1 ♀, HI: Oahu, Manoa Stream, cone case, 29.viii.2003 Emerg[e]d: 16.ix.2003 (2 ♂, one dissected PS163), 11.ix.2003 (1 ♀), [Daniel] Rubinoff; 1 ♀, HI: Oahu, Manoa Stream, coll[ection]: V-03, Em[erge]d: 18.viii.2003, Rubinoff, coll[ector].; 14 ♂, 8 ♀, HI: Oahu Isl[and]., 'cone', Kalauao Stream, 25.i.2004, Em[erge]d: 21/22.iv.2004 (11 ♂, 6 ♀),

23.iii.2004 (1 ♂, dissected PS159), 8/15.iv.2004 (1 ♂, dissected PS164, 2 ♀, one dissected PS153), 27.iv.2004 (1 ♂), Rubinoff, coll. Deposited in BPBM, MHNG, UHIM, and USNM.

Diagnosis: Amongst the species of *Hypasmocoma*, *H. kahamanoa* is very similar to *Hypasmocoma sacco-phora* Walsingham, 1907, also endemic to the island



Figure 2. Cone case types of aquatic *Hyposmocoma* spp., larvae. A, *Hyposmocoma kahamanoa* sp. nov., lateral aspect; B, *Hyposmocoma kawaiikoi* sp. nov., lateral aspect; C, *Hyposmocoma wailua* sp. nov., dorsal aspect.

of Oahu, in size and forewing pattern. However, it differs in males in having a shorter sclerotized hook on abdominal segment VII and in male genitalia in having sclerotized spur-like setae of different shape and length on each valva. Although the number of setae can vary amongst different specimens of *H. kahamanoa*, the setae on the right valva are $1/2 \times$ the length and on the left valva are thick and slightly curved apically and $2 \times$ the length of those found in *H. saccophora*. *Hyposmocoma kahamanoa* differs from *Hyposmocoma kahaiao* sp. nov., *Hyposmocoma kawaiikoi* sp. nov., and *Hyposmocoma uhauiole* sp. nov. in the characters mentioned in the Diagnosis and Description of these species, below.

Description: Male ($N = 25$) (Figs 1A, 5). Wingspan 7.6–9.0 mm (holotype: 9.0 mm). Head adorned with large, shiny, dark grey scales on occiput becoming beige on vertex and frons. Haustellum with beige scales. Maxillary palpus reduced. Recurved labial palpus mostly dark grey dorsally and beige ventrally with some sparse beige scales on segments, and on second segment apically. Antennal flagellum dark grey; scape dark grey with beige scales ventrally and forming disrupted ring apically, antennal pecten present with up to four thin setae. Thorax, tegula, and metascutellum dark grey. Foreleg coxa beige; femur dark grey; tibia and tarsomeres dark grey with beige ring at middle and apex of tibia, and apex of tarsomeres I, II. Midleg as foreleg, spurs beige. Hindleg as midleg, but ground colour more silver grey. Forewing dark grey with sprinkling of dark grey scales on a pale beige background, dark grey markings as pair of spots medially (often fused in darker specimens), disconnected from each other along diagonal, and a more or less conspicuous small spot post-

medially in midline; cream markings as a small notch subapically on costal margin and another opposite on inner margin. Hindwing and fringe uniformly silver grey. Subcostal brush absent. Abdomen dorsally dark grey; ventrally beige, with tuft of long beige scales on each side of genitalia. Sclerotized hook (pseuduncus *sensu* Zimmerman, 1978) small with distinct sclerotized ring on segment VII. Genital flaps (epitrygmata *sensu* Zimmerman, 1978) membranous, rounded, broad and thin, emerging on both sides apically of sclerotized sternum VIII.

Male genitalia ($N = 4$) (Fig. 5). Uncus and gnathos absent, but replaced by uncus-like processes attached to tegumen (brachia *sensu* Zimmerman, 1978), right process elongate and thin, sickle-shaped, curved ventrally, apically pointed, with small notch at $1/3$ length, about $8 \times$ length of left process. Tegumen wide, heavily sclerotized, dorsoventrally flattened. Valvae symmetrical, with long and slender arms, enlarged apically, bent upward in the middle, adorned with setae arranged comb-like along dorsal margin, with sclerotized spur-like setae of same length apically rounded on right valva, and large sclerotized spur-like setae on left valva, being $6 \times$ length of those on right valva; number of spur-like setae vary amongst specimen studied, three right and three left, three right and two left, or two right and two left. Phallus large, heavily sclerotized, slightly bent to the right, blunt tipped, with large bulbous base; vesica without spines or cornuti. Anellus with two symmetrical lobes, thin, angled upward, both adorned with small setae until apex, right lobe very slightly enlarged apically.

Female ($N = 15$). Wingspan 8.8–9.8 mm. Frenulum with three acanthae. Forewing background colour dark grey with indistinct dark grey markings. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 11A). Papillae anales short. Apophyses thin and straight; posterior apophyses, very long about $5 \times$ length of anterior apophyses. Ostium-bearing process heavily sclerotized and very large, externally protruding, snail-shell shaped curled to the left, with broad base. Ductus bursae long and of small girth. Corpus bursae oval and elongate, with light scobination; signum absent. Inception of ductus seminalis very enlarged, cylindrical, situated behind of corpus bursae. Apical margin of sternum VII with broad U-shaped emargination medially forming a bowl encompassing ostium-bearing process with patches of dense scales situated laterally.

Larva (Figs 3, 4). Length 4.5–5.0 mm ($N = 58$). Body pale yellow, textured with microconvolutions; head capsule amber; prothoracic shield amber, gradually darkening posteriorly, mesothorax and metathorax with pale amber patches similar to prothoracic shield; pale brown patches on thoracic segments as a hori-

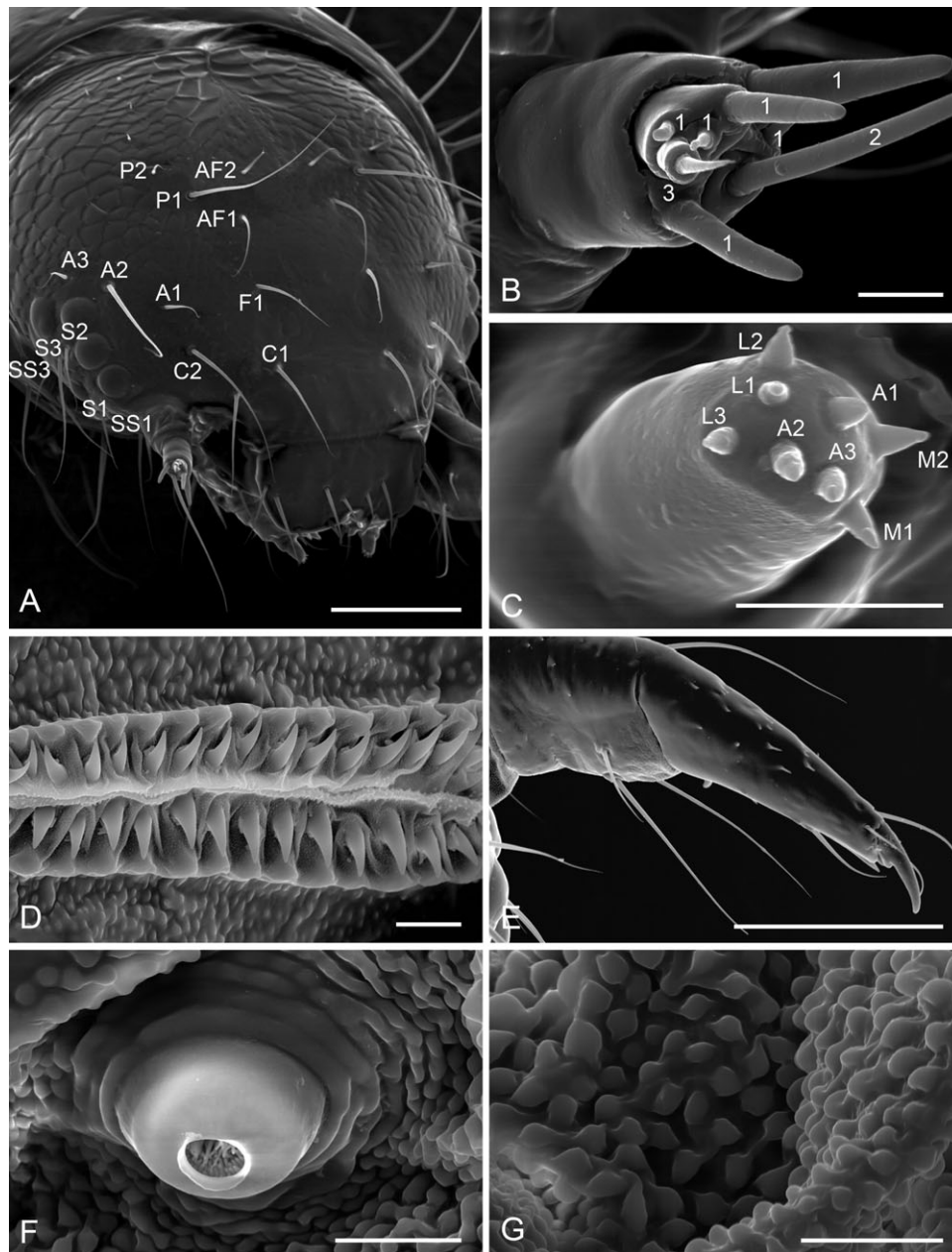


Figure 3. Scanning electron micrographs of larva of *Hyposmocoma kahamanoa* sp. nov. A, frontolateral view of head capsule, scale bar = 100 μ m; B, sensilla of antenna: 1 = sensilla basiconica, 2 = sensillum chaetica, 3 = sensillum styloconicum, scale bar = 10 μ m; C, sensilla of maxillary palpus: A2 = sensillum styloconicum, A1, A3, M1–2, L1–3 = sensilla basiconica, scale bar = 10 μ m; D, left proleg on abdominal segment 4, scale bar = 10 μ m; E, distal portion of left prothoracic leg showing claw, scale bar = 100 μ m; F, left spiracle on abdominal segment 5, scale bar = 10 μ m; G, detail of the hydrophilic microstructure of the cuticle, scale bar = 10 μ m. Seta designations: A, anterior; AF, adfrontal; C, clypeal; P, parietal; S, stemmatal; SS, substemmatal. Sensilla designations: A, apical; L, lateral; M, medial.

zontal elongated patch in middle and a perpendicular elongated patch posterior to coxa (on some larvae inconspicuous); pinacula pale yellow; anal plate amber; setae with pale brown, circular, and very slightly raised sockets. Head (Figs 3A–C, 4D): semi-

hypognathous, textured with slightly raised, confluent, polygonal ridges except on area between adfrontal sclerites (Fig. 4A); adfrontal sclerites widened distally, frontal setae about equal in length, AF2 above apex of frons, AF1 below; F1 slightly closer

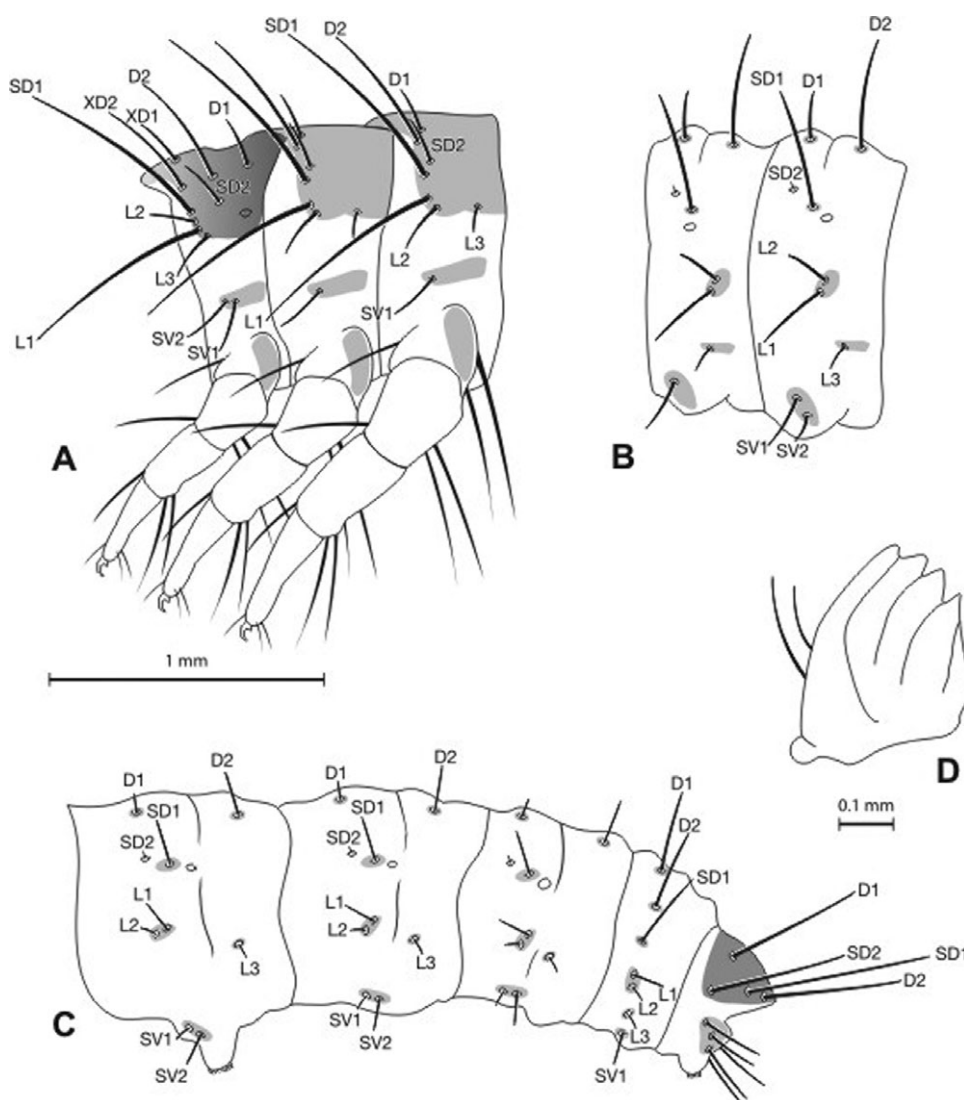


Figure 4. Larva of *Hyposmocoma kahamana* sp. nov. A, chaetotaxy of thorax; B, chaetotaxy of abdominal segments 1–2; C, chaetotaxy of abdominal segments 6–10; D, mandible. Seta designations: D, dorsal; L, lateral; SD, subdorsal; SV, subventral; XD, supernumary dorsal.

to AF1 than to C1, AF1 and F1 at least two \times longer than AF2; C1 and C2 of same length; clypeus with five pairs of setae, three pairs on medial half, two on distal half; mandible simple (Fig. 4D), shallowly notched, bearing pair of subequal setae on outer surface near condyle, and with four distinct distal teeth; sensilla types and arrangement on antenna (Fig. 3B) and on maxillary palpi (Fig. 3C) similar to those of other Gelechioidea (for references, see Schmitz & Landry, 2006). Six stemmata in genal area, arranged in an arc with six caudad, stemmata 2, 3, 4 close together in straight line with stemma 5 separated from 4, 6 by width of a stemma; substemmata setae about equal in length; S3 posteroventrad to S2, S2 approximate to stemma 3, and S1 approxi-

mate to stemma 5; A-group setae above gena, A1 and A3 at least three \times longer than A2; L1 very short and posterodorsad to stemma 2; P1 anteroventrad to AF2, P2 posterodorsad to P1, P1 about seven to eight \times longer than P2. Thorax (Figs 3E, 4A): T1 with L-group trisetose, surrounded by prothoracic shield; setae anterior to spiracle; L1 in between and equidistant to L2 and L3, about 2.5 \times lengths of L2 and L3; SV-group setae of same length on anterior part of elongate pinaculum; coxae nearly touching, V1s posteroventrad of coxae; segments of leg smooth, very long, with sparse hair-like spines, claw single (Fig. 3E); shield with SD1 in straight line with XD2 and XD1; SD1 about same length then L1; XD2 and D2 about equal in lengths; XD2 about 2.5 \times length of

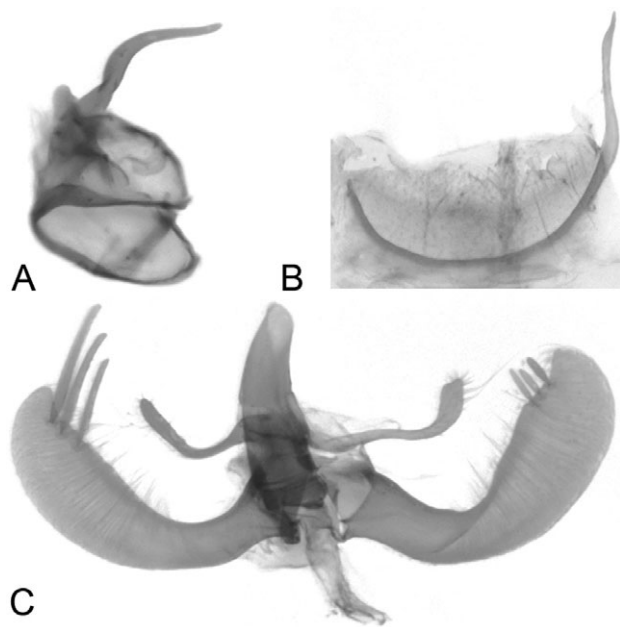


Figure 5. Male genitalia of *Hyposmocoma kahamanoa* sp. nov. from specimen on slide PS163. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

XD1, at same distance from XD1 as from SD1; XD1 about same length as D1 and SD2; D1 in straight line with D2 and XD2, posterior to SD2 and D2; SD2 in straight line with SD1. T2–T3 (Fig. 4A): D2 about two \times length of D1, both on small pinaculum; SD1 about five \times length of SD2, both on small pinaculum; L1 about three \times longer than L2, both on small pinaculum, L3 slightly shorter than L2, posterior to or in vertical line with SV1; D1, D2, SD1, SD2, L1, and L2 surrounded by pale brown patch similar to prothoracic shield; SV1 on anterior part of elongated pale brown patch; V1s on T2–T3 about equal distance apart (not shown), at least 1.5 \times distance between V1s on T1. Abdomen (Figs 3C, F, G, 4B, C): A1–A2 (Fig. 4B): D2 about 1.5 \times length of D1; SD1 above spiracle on A1, and slightly anterodorsad to spiracle on A2, about of same length than D2; SD2 minute and anterodorsad to SD1; spiracle on A1 of same size than those on A2–A7; L1 about five \times length of L2, both on same pinaculum, below and slightly posterior to spiracle; L3 about same length as L2, posterior to, or in vertical line with L1 and L2; SV-group unisetose on A1 and bisetose on A2, on same pinaculum; V1s equal distance apart (not shown), at least two \times distance between V1s on T2–T3. A3–A10 (Figs 3C, F, 4C): A3–A6 with four pairs of little prominent prolegs, crochets uniordinal, in ellipse (Fig. 3C); setae as A1–A2, except all setae at least only half the size; A7 as A3–A6, except L3 closer to L1 and L2; A8 as A7

except spiracle slightly larger than on previous segments (Fig. 4C); A9 with D1, D2, and SD1 of equal lengths and in straight line, with D2 equidistant to both setae; L-group setae also nearly in straight line with D1, D2, and SD1; L1 small, about two \times length of L2, on same pinaculum; L3 of same length as L2; SV1 slightly shorter than L1; V1s as previous segments; A10 (Fig. 4C): anal plate with D1, D2, and SD2 equal in lengths, SD1 slightly longer; crochets of proleg uniordinal, in ellipse.

Larval case ($N = 290$) (Fig. 2A). Cone-shaped structure, 7.0–12.5 mm in length, cases of young larvae may be very small (< 1.0 mm), small and thin, decorated with beige, brown, and black bits of sand woven with silver silk filaments; bicoloured, paler beneath and darker above, dorsally brown silk peppered with varying degrees of black usually resulting in dark brown overall colour, dorsal side encrusted with lichen, algae, and diatoms giving a coarse appearance, ventral side silver and remarkably smooth with occasional black mottling; aperture of case covered with an operculum decorated with small pebbles, or sand grain fastened by silk, that can be closed tidily by the larvae with its mandibles from the inside; background colour ranging from dark brown to black.

Etymology: The name *H. kahamanoa* is derived from the Hawaiian, *kaha*, edge, that refers to the edge of the stream habitat, and the Mānoa stream, which flows through the Mānoa Valley on the island of Oahu, where this species was collected for the first time by D. R. in 2004.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in streams on the island of Oahu in January, April, May, and August, and are probably present year round. They were found above and under the water line mostly in small holes covering the porous volcanic rocks, always at places where the sun breaks through the tree canopy, probably promoting the growth of algae and lichens on the rocks. Heavily shaded areas of the streams do not appear to be suitable habitat for the larvae. Adults can be observed during the day, but apparently are not attracted to light even if a black light trap is placed beside a stream where they occur abundantly.

The larvae rest on emergent rocks in the middle and edges of the streams where they feed on lichens, and especially fresh and dried algae, but they can also dive for long periods of time in order to feed on algae. When under water they secure themselves with silk, which can be used by the larva as a life-line if it becomes dislodged by pulling on the strand in order to reattach to the rock. The most likely explanation for the respiration strategy is a direct diffusion of oxygen

through the hydrophilic skin along the abdomen. This is supported by the fact that no tracheal gills were observed on the body of the larvae like those found for example in aquatic species of Acentropinae (Solis, 2008). In addition, temporary oxygen storage in the form of a trapped air bubble in the case was found rarely, despite multiple dissections ($N=20$). The tracheal system appears to be unmodified with no reduction in the diameter of the spiracles, being morphologically open (Fig. 3F), that might confer on the larvae a peripneustic tracheation (Welsh, 1922). Additionally, details of the exocuticle, or integument (Fig. 3G), show that it is smooth with simple rounded protuberances of the cuticular surface (Reichholf, 1976), rather than composed of tiny hydrophobic cuticular hair-like structures, also called microtrichia (Solis, 2008), that make up the plastron of hydrophobic larvae in species of Acentropinae (Wichard, Arens & Eisenbeis, 2002; Speidel, 2005; Solis, 2008). Therefore, the combination of the small size of the larvae, their occurrence strictly in well-oxygenated, fast-moving streams, and the hydrophilic microstructure of their cuticle suggests that the aquatic larvae probably rely on direct diffusion when submerged. Laboratory experiments confirm that the larvae die quickly in stagnant water (in a matter of hours), but are able to survive for weeks forcibly submerged in a well-oxygenated aquarium (Rubinoff & Schmitz, 2010).

Distribution: Known only from streams (Manoa, Palolo, Kaluaao streams and certainly others) in the Ko'olau mountains of eastern Oahu where it is presumed to be endemic.

Remarks: Based on differences in male genitalia, this species may represent the new species 26 of Zimmerman (1978) collected near the head of Kawailoa Gulch in the Ko'olau range and described (mistakenly according to Zimmerman) by Walsingham (1907) as a paratype of *H. saccophora*. We are supported in our observation by the fact that *H. kahamanoa* seems to be endemic to the Ko'olau range on east Oahu, whereas *H. saccophora* appears to be endemic to the Waianae range on west Oahu. Finally, the two Oahu species are not only allopatric but ecologically very different; *H. kahamanoa* is strictly aquatic, being found in and around streams of the Ko'olau range, whereas *H. saccophora* inhabits dry open rocky terrain in the Waianae mountains. Parasitoids were reared from some larvae and have been identified as belonging to the Eupelmidae ($N=2$) and Pteromalidae ($N=2$) (Hymenoptera: Chalcidoidea).

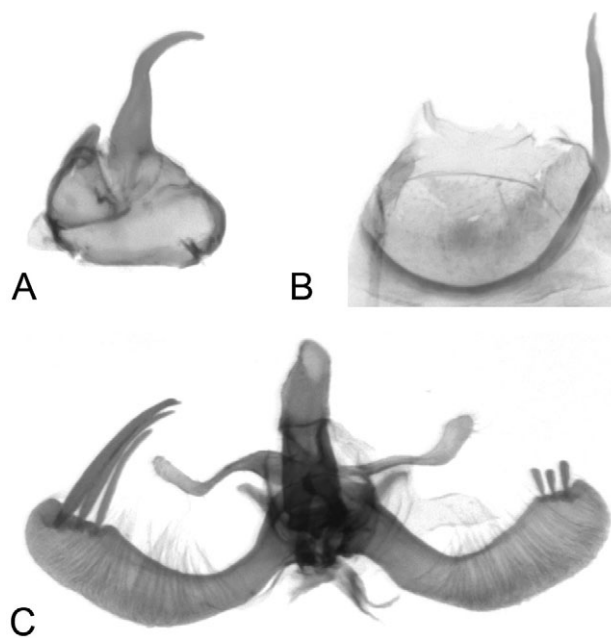


Figure 6. Male genitalia of *Hyposmocoma uhauiole* sp. nov. from specimen on slide PS154. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

***HYPOSMOCOMA UHAUIOLE* SCHMITZ & RUBINOFF
SP. NOV. (FIGS 1B, 6, 11B)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, Uhaui'ole Stream | 'cone' case, VIII-8-[20]07 | em[ergence]. X-31-[20]07, #DR07H1A | leg[it]. D[aniel]. Rubinoff, W[ill]. Haines'; [2] 'HOLOTYPE | Hyposmocoma | uhauiole | Schmitz and Rubinoff'. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 16 ♂, 23 ♀, from Kauai Island, Hawaii, USA; 5 ♂, 13 ♀, with same data as holotype except date of emergence: 16.viii.2007 (1 ♀), 17.viii.2007 (1 ♀, dissected PS143), 18.viii.2007 (1 ♀), 19.viii.2007 (1 ♀), 21.viii.2007 (1 ♀), 26.x.2007 (2 ♀), 31.x.2007 (1 ♀), 7.xi.2007 (1 ♂, 1 ♀), 26.xii.2007 (2 ♂, one dissected PS142), 2.i.2008 (2 ♂, dissected PS154 and PS160), 8.i.2008 (1 ♀), 30.i.2008 (1 ♀); 1 ♂, 2 ♀, HI: Kauai Island, Uhaui'ole Stream, among rocks, 8.viii.2007, Haines, Rubinoff, coll.; 2 ♂, 2 ♀, HI: Kauai, Uhaui'ole St[rea]m., 7.4 mi[les] from Kuamo'o R[oa]d., 27.ii.2004, 'cone', Em[e]rg[ed]. 4.v.2004 (2 ♂), 12.v.2004 (1 ♀), 27.v.2004 (1 ♀), Rubinoff, coll.; 1 ♀, HI: Kauai, Uhaui'ole Stream, ii.2004, Emerg[e]d. 26.iii.2004, Rubinoff, coll.; 9 ♂, 6 ♀, HI: Kauai, N. Fork of Wailua river, N 22.06269°, W 159.46791°, elev[ation]. 1186 f[eet], 'cone' case, 23.ii.2009, em[ergence]. 20.iii.2009 (1 ♀), 28.iii.2009 (2 ♀), 29.iii.2009 (1 ♂, 1 ♀), 30.iii.2009 (8 ♂, 2 ♀), #DR09B4A, coll[ectors]. P[atrick]. Schmitz, D[aniel].

Rubinoﬀ, M[ichael]. San Jose; 1 ♂, HI: Kauai, Keahua stream, N 22.07143°, W 159.41765°, elev. 607 ft, 'cone' case, 23.ii.2009, em. 4.iv.2009, #DR09B6A, coll. P. Schmitz, D. Rubinoﬀ, M. San Jose; 1 ♀, HI: Kauai, Uhauiole stream, N 22.06557°, W 159.42076°, elev. 613 ft, 'cone' case, 23.ii.2009, em. 25.iii.2009, #DR09B5A, coll. P. Schmitz, D. Rubinoﬀ, M. San Jose. Deposited in BPBM, MHNG, UHIM, and USNM.

Diagnosis: *Hypsmocoma uhauiole* is most similar in forewing markings to *H. kahamanoa* sp. nov., *H. kahaiao* sp. nov., and *H. saccophora* Walsingham, 1907, but it differs from these species in that the males have a thick sclerotized ring and sclerotized hook on abdominal segment VII, and in that the male genitalia have small rounded sclerotized spur-like setae on the right valva and very long setae on the left valva.

Description: Male ($N = 17$) (Figs 1B, 6). Wingspan 6.5–7.9 mm (holotype: 7.8 mm). As *H. kahamanoa*, except forewing uniformly dark grey, sometimes with very few scattered white scales, with no distinct markings, although on some specimens the dark grey and/or cream markings can be more or less visible.

Male genitalia ($N = 1$) (Fig. 6). As for *H. kahamanoa*, except for valvae with three rounded spur-like setae on right valva and three on left valva sequentially longer distally, being four to six × the length of those on right valva.

Female ($N = 23$). Wingspan 7.1–9.0 mm. As *H. kahamanoa*, except forewing uniformly dark grey.

Female genitalia ($N = 1$) (Fig. 11B). As for *H. kahamanoa*, except for posterior apophyses about 3.5 × length of anterior apophyses.

Larval case ($N = 247$). Cone-shaped structure, 7.0–8.0 mm in length, as *H. kahamanoa*, except case ventrally not as smooth, with more texture underneath and more a dull white than silver colour. Cases frequently less straight than *H. kahamanoa* giving the case a less angular, more irregular appearance.

Etymology: The name *H. uhauiole* is derived from the Uhauiole stream on the eastern side of the island of Kauai where this species can be found.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae can be collected day or night on rocks in streams on the island of Kauai in February and August, but probably occur nearly year-round. The larvae of this moth can be seasonally abundant on rocks along the shoreline and in the middle of the streams where they occur. Moths were often seen flying between emergent rocks and crawling actively on them during the day. This species

is partially sympatric and synchronic with *Hypsmocoma ipowainui* and *Hypsmocoma wailua*, a burrito and a bugle-cased species, respectively (see below for species descriptions). The exact range of this species is not clear, although it is replaced by the superficially similar species, *H. kawaikoi*, on the western side of Kauai, from which *H. uhauiole* is quite genetically distinct (Rubinoﬀ, 2008). This suggests historical barriers to gene flow confirming at least the partial allopatry that we observed. Initial genetic data suggest the possibility of a cryptic species within the *H. uhauiole* lineage, but we were unable to see any corresponding morphological divergence and leave this issue for future research.

Distribution: Known only from various streams (Uhauiole, Wailua, and Keahua streams) found on the eastern side of the island of Kauai where it appears to be endemic.

Remarks: This species can be abundant on and under rocks in and near flowing water but frequents small and large rocks, unlike the burrito-cased sympatric species, which seems to prefer large boulders, avoiding smaller rocks. Preliminary COI sequence data suggests a cryptic cone-cased sympatric species, but we have yet to find morphological characters to support any division.

HYPSMOCOMA KAHAILO SCHMITZ & RUBINOFF SP. NOV. (FIGS 1C, 7, 11C)

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Maui, Iao Valley Stream | 'cone' case, III-27-[20]06 | em[ergence]. V-23-[20]06, #DR06C12b | leg[it]. D[aniel]. Rubinoﬀ; [2] 'HOLOTYPE | *Hypsmocoma* | kahaiao | Schmitz and Rubinoﬀ. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 11 ♂, 21 ♀, from Maui Island, Hawaii, USA; 6 ♀, same data as holotype except date of emergence: 28.iv.2006, 13.vi.2006, 14.vii.2006, 30.vi.2006, 11.viii.2006, 19.viii.2006; 4 ♀, HI: Maui, Iao Valley Stream, 'cone' case, 24.ix.2005, em[ergence]. 16.i.2005, 25.ii.2006, 2.iii.2006, 9.iii.2006, #DR05I3, leg. D. Rubinoﬀ; 11 ♂, 11 ♀, HI: West Maui, Maui Land and Pineapple, Honolua Stream, elev[ation]. 900 m, 'cone' case, 6.i.2006, em. 25.ii.2006 (1 ♂, 1 ♀), 27.ii.2006 (1 ♂), 2.ii.2006 (2 ♂), 2.iii.2006 (1 ♂, dissected PS162, 3 ♀), 4.iii.2006 (1 ♂), 9.iii.2006 (2 ♂, 5 ♀), 23.iii.2006 (1 ♂), 3.iv.2006 (2 ♀), 12.iv.2006 (2 ♂, one dissected PS157), #DR06A7. Deposited in MHNG, UHIM, and USNM.

Diagnosis: *Hypsmocoma kahaiao* is most similar in forewing markings to *H. kahamanoa* sp. nov., *H. uhauiole* sp. nov., and *H. saccophora* Walsingham,

1907, but it differs from these species in males in having a short sclerotized hook, and in female genitalia in having a small and thin ostium-bearing process, and from *H. kahamanoa* and *H. uhauiole* in male genitalia in having thin sclerotized spur-like setae on each valva.

Description: Male ($N = 12$) (Figs 1C, 7). Wingspan 6.8–7.7 mm (holotype: 7.7 mm). As *H. kahamanoa*, except antennal pecten present with up to two thin setae, forewing dark grey with sprinkling of dark grey scales on an off-white background, off-white markings as a small notch subapically on costal margin and another opposite on inner margin, abdomen dark brown with tuft of long dark brown scales on each side of genitalia, and sclerotized hook small with indistinct sclerotized ring on segment VII.

Male genitalia ($N = 3$) (Fig. 7). As for *H. kahamanoa*, except for valvae asymmetrical with right valva slightly larger at apex with two rounded sclerotized spur-like setae of same length apically (sometimes one thinner in the middle), and small subapical triangular projection bearing distant spur-like setae, left valva with large sclerotized spur-like setae, being three to four \times length of those on right valva; number of spur-like setae vary amongst specimen under scrutiny, two of same length, or four, with two thinner spur-like setae on each side, right lobe of anellus very slightly enlarged apically.

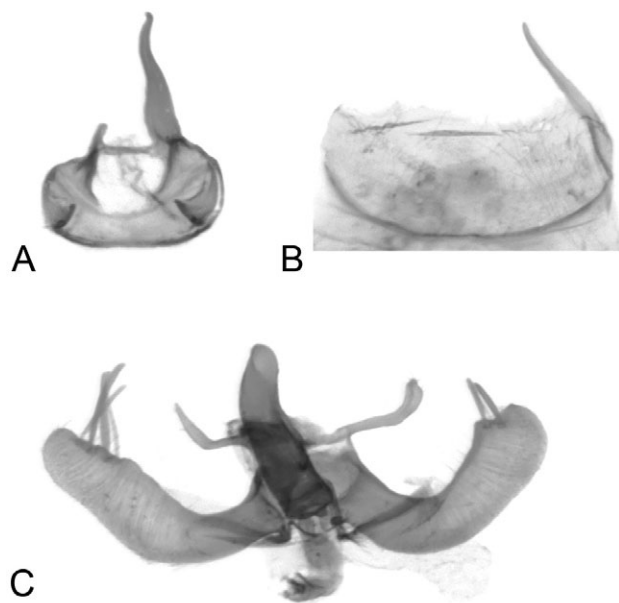


Figure 7. Male genitalia of *Hyposmocoma kahaiao* sp. nov. from specimen on slide PS162. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

Female ($N = 21$). Wingspan 7.2–10.3 mm. As *H. kahamanoa*, except for forewing background colour dark grey with indistinct dark grey markings.

Female genitalia ($N = 1$) (Fig. 11C). As for *H. kahamanoa*, except for posterior apophyses about 3.5 \times length of anterior apophyses, ostium-bearing process small and thin, and apical margin of sternum VII with broad V-shaped emargination medially.

Larval case ($N = 84$). Cone-shaped structure, 7.0–10.5 mm in length, as *H. kahamanoa*, except that there are often a few small pebbles attached at case entrance.

Etymology: The name *H. kahaiao* is derived from the Hawaiian, *kaha*, edge, that refers to the edge of the stream habitat, and, from the Iao stream on the western end of the island of Maui where this species can be found.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in streams on the island of Maui in January, February, and September. In Honolulu stream, this species was frequently observed resting in large numbers on the undersides of submerged rocks. Whereas other aquatic species were occasionally found submerged, this species may choose to rest underwater more frequently. Future research may indicate that thermal regulation is part of the reason for this behaviour, as this is one of the warmer locations where we found aquatic larvae.

Distribution: Known only from the Hawaiian island of Maui, presumed to be endemic to the streams of the west Maui volcano (Iao and Honolulu streams).

Remarks: This species may represent the youngest and farthest east aquatic cone species because the only other cone-cased species of which we are aware is on east Maui (reared, but currently undescribed) and does not appear to be aquatic.

***HYPOSMOCOMA KAWAIKOI* SCHMITZ & RUBINOFF
SP. NOV. (FIGS 1D, 2B, 8, 11D)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, Kawaiikoi stream | N 22.13158°, W 159.62161° | elev[ation]. 3490 f[ee]t, 'cone' case, II-24-[20]09 | em[ergence]. IV-6-[20]09, #DR09B7A | coll[ectors]. P[atrick]. Schmitz, D[aniel]. Rubinoff | M[ichael]. San Jose'; [2] 'HOLOTYPE | Hyposmocoma | kawaiikoi | Schmitz and Rubinoff. Specimen in perfect. Deposited in the UHIM.

PARATYPES: 18 ♂, 10 ♀, from Kauai Island, Hawaii, USA; 4 ♂, with same data as holotype except date of emergence; 14 ♂, 10 ♀, with same data as

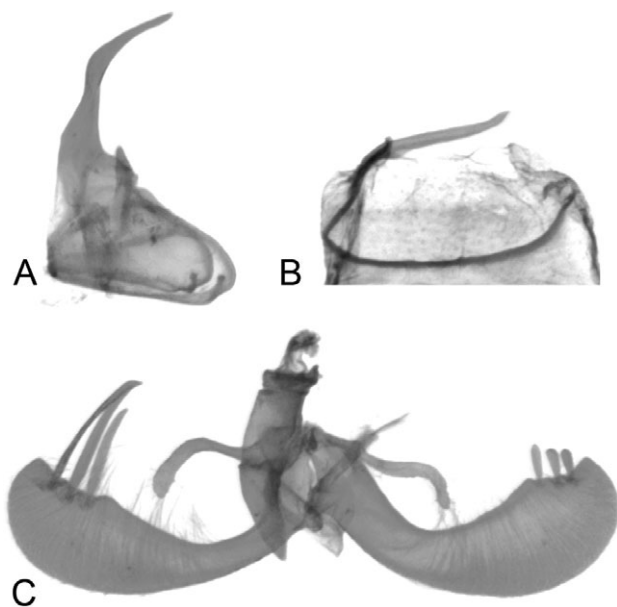


Figure 8. Male genitalia of *Hyposmocoma kawaikoi* sp. nov. from specimen on slide PS198. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, dorsal aspect; C, valvae with phallus, ventral aspect.

holotype except date of emergence: 31.iii.2009 (2 ♂), 1.iv.2009 (1 ♂, 1 ♀), 3.iv.2009 (2 ♂), 9.iv.2009 (2 ♂, 2 ♀), 10.iv.2009 (3 ♂), 13.iv.2009 (3 ♂, one dissected PS198, 3 ♀, one dissected PS199), 14.iv.2009 (1 ♂, 1 ♀), 16.iv.2009 (3 ♀). Deposited in MHNG, UHIM, and USNM.

Diagnosis: *Hyposmocoma kawaikoi* is a mostly uniform dark grey species. Based on external and genital characters, it can be easily separated from the closest looking species, *H. kahaiaoa* sp. nov., *H. kaha-manooa* sp. nov., *H. saccophora* Walsingham, 1907, and *H. uhauiole* sp. nov. by its more uniform background colour, and the broad valvae in males.

Description: Male ($N = 19$) (Figs 1D, 8). Wingspan 9.3–10.3 mm (holotype: 10.1 mm). As *H. kaha-manooa*, except antennal pecten present with up to seven thin setae, forewing ground colour mostly dark grey with some scattered off-white and light bluish tinge scales, off-white markings as a large notch subapically on costal margin and another opposite on inner margin.

Male genitalia ($N = 1$) (Fig. 8). As for *H. kaha-manooa*, except for valvae with three rounded spur-like setae on right valva and three on left valva sequentially longer distally being six \times length of those on right valva.

Female ($N = 9$). Wingspan 9.8–10.7 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 11D). As for *H. kaha-manooa*, except for posterior apophyses about $3.5 \times$ length of anterior apophyses.

Larval case ($N = 45$) (Fig. 2B). Cone-shaped structure, 6.0–7.0 mm in length, large and broad, decorated with bits of dark grey sand woven with silver silk filaments; bicoloured, paler beneath and darker above; aperture of case covered with an operculum decorated with small beige, brown, white, and black pebbles fastened by silk, can be closed neatly and tightly by the larvae with its mandibles from the inside; case has silk extensions laterally from each side of the aperture giving the appearance of horns; pebbles extend on dorsal side until about half of the case; background colour ranging from grey to dark brown.

Etymology: The name *H. kawaikoi* is derived from the Kawaikoi stream in the Alaka'i swamp on the island of Kauai where this species can be found.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in streams on the island of Kauai in February, and have been observed in May and August as well. These larvae are frequently found on relatively small, barely emergent rocks in fast flowing torrents. The climate at this high elevation site is much cooler and even wetter (nearby areas average over 10 m of rain per year) than the Wailua river area on the east side of Kauai. Although the larvae of Kawaikoi are found year round, temperatures can approach freezing in this location. This is not the case for the lower elevation Wailua river area of Kauai, which remains much more tropical year round.

Distribution: Known only from the Kawaikoi stream that drains the Alaka'i swamp on the north-western plateau of the island of Kauai where it is presumed to be endemic.

Remarks: This aquatic species has the largest cone-cased larva, easily distinguished from the sympatric bugle-cased larva of *H. eepawai* (see Fig. 14A), also restricted to the Kawaikoi stream.

***HYPSMOCOMA KAMAKOU* SCHMITZ & RUBINOFF SP. NOV. (FIGS 1E, 9, 11E)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Molokai, Kamakou Pres[erve]. | stream at Kawela Gulch | 'cone' case, V-20-[20]04 | em[ergence]. VII-6-[20]04 | coll[ector]. D[aniel]. Rubinoff'; [2] 'HOLOTYPE | *Hyposmocoma* | kamakou | Schmitz and Rubinoff. Specimen in good condition except for broken antennae. Deposited in the UHIM.

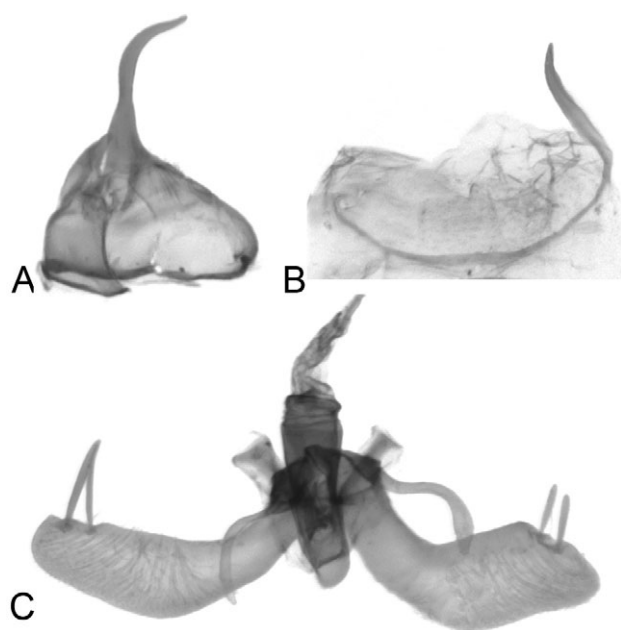


Figure 9. Male genitalia of *Hyposmocoma kamakou* sp. nov. from specimen on slide PS166. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

PARATYPES: 5 ♂ (one dissected PS 166), 3 ♀ (one dissected PS 167), from Molokai Island, Hawaii, USA, with same data as holotype. Deposited in BPBM, UHIM and USNM.

Diagnosis: *Hyposmocoma kamakou* can be confused based on forewing pattern only with the somewhat similar *H. wailua* sp. nov. in the genus, but can be separated from the latter by the thin sclerotized ring and the short sclerotized hook on abdominal segment VII in males and by the thinner valvae, and the shape of sclerotized spur-like setae in male genitalia.

Description: Male ($N = 6$) (Figs 1E, 9). Wingspan 6.8–8.4 mm (holotype: 7.6 mm). As *H. kahamanoa*, except background colour of forewing off-white with light bluish tinge scales, and sclerotized hook long with pointed apex.

Male genitalia ($N = 1$) (Fig. 9). As for *H. kahamanoa*, except for valvae with three rounded spur-like setae, the one in the middle being very thin on right valva and two of same length on left valva being three \times length of those on right valva.

Female ($N = 3$). Wingspan 8.3–10.4 mm. As *H. kahamanoa*, except background colour of forewing off-white with light bluish tinge scales.

Female genitalia ($N = 1$) (Fig. 11E). As for *H. kahamanoa*, except for posterior apophyses about 3.5 \times

length of anterior apophyses, ostium-bearing process small and thin, and apical margin of sternum VII not emarginated.

Larval case ($N = 60$). Cone-shaped structure, 6.0–9.0 mm in length, as *H. kahamanoa*.

Etymology: The name *H. kamakou* is derived from the Kamakou Preserve on the island of Molokai managed by The Nature Conservancy.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in streams on the island of Molokai in May.

Distribution: Known only from the high elevation streams of The Nature Conservancy's Kamakou preserve on the island of Molokai where it is presumed to be endemic.

Remarks: This species may be found to have a broader distribution in the mountain streams of Molokai but the difficulty of gaining access to these streams limited our ability to assess thoroughly the range of *H. kamakou*. However, Liebherr (1997) found that carabid beetle diversity was unexpectedly high and complex in the mountains of Molokai, so additional species may be expected in aquatic *Hyposmocoma* as well. Although both species are inhabiting the streams of the island of Kauai, *H. kamakou* and *H. wailua* occur in allopatry.

***HYPSMOCOMA WAILUA* SCHMITZ & RUBINOFF**

SP. NOV. (FIGS 1F, 2C, 10, 11F)

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, N. Fork of Wailua river | N 22.06269°, W 159.46791° | elev[ation]. 1186 feet, 'bugle' case, II-23-[20]09 | em[ergence]. IV-20-[20]09, #DR09B4B | coll[ectors]. P[atrick]. Schmitz, D[aniel]. Rubinoff, M[ichael]. San Jose'; [2] 'HOLOTYPE | *Hyposmocoma* | *wailua* | Schmitz and Rubinoff'. Specimen in perfect condition. Deposited in the UHIM.

PARATYPES: 6 ♂, 7 ♀, from Kauai Island, Hawaii, USA; 1 ♂, with same data as holotype; 5 ♂, 7 ♀, with same data as holotype except date of emergence: 2.iii.2009 (1 ♂), 2.iv.2009 (1 ♀), 3.iv.2009 (1 ♂), 6.iv.2009 (1 ♂, 1 ♀), 7.iv.2009 (1 ♂, dissected PS200, 1 ♀), 9. iv.2009 (2 ♀), 10.iv.2009 (1 ♀, dissected PS201), 13.iv.2009 (1 ♀), 20.iv.2009 (1 ♂). Deposited in BPBM, UHIM, and USNM.

Diagnosis: *Hyposmocoma wailua* is a relatively small uniform greyish-blue species with metallic blue iridescences. Adults can be easily distinguished from the closest looking species, *H. kamakou* sp. nov., by the

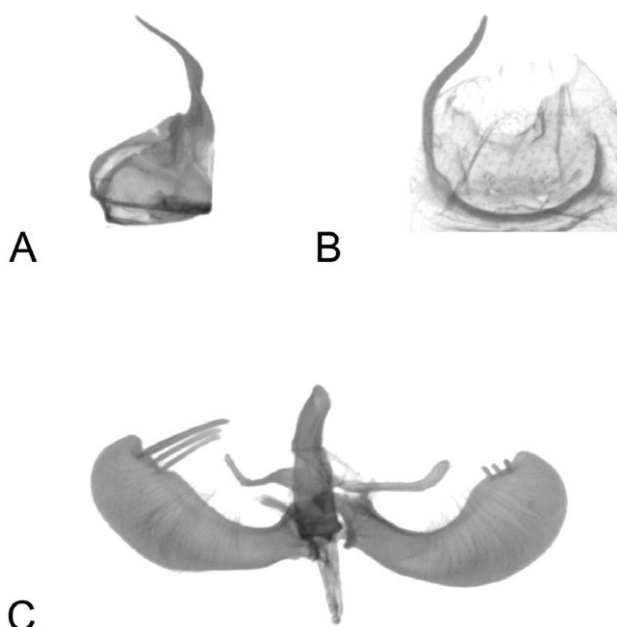


Figure 10. Male genitalia of *Hyposmocoma wailua* sp. nov. from specimen on slide PS200. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, dorsal aspect; C, valvae with phallus, ventral aspect.

broad valvae and differences in shape and length of the sclerotized spur-like setae in male genitalia, and distinct sclerotized ring and minute sclerotized point on abdominal segment VII in males. The larvae of these two species have easily distinguished case types (Fig. 2A, C).

Description: Male ($N = 7$) (Figs 1F, 10). Wingspan 7.9–9.3 mm (holotype: 8.1 mm). Head with greyish-blue scales converging to occiput becoming off-white on vertex and frons. Haustellum with greyish-blue scales. Maxillary palpus reduced. Labial palpus recurved with greyish-blue scales dorsally and off-white scales ventrally. Antenna flagellum darkish grey; scape with greyish-blue scales and off-white ring at apex; antennal pecten present with three to six thin setae. Thorax greyish-blue; metascutellum greyish-beige. Foreleg greyish-blue. Midleg as foreleg, but also with inconspicuous off-white ring on apex and middle of tibia, and tarsomeres I–II, spurs pale beige. Hindleg as midleg, but ground colour pale greyish blue. Forewing greyish blue with some scattered off-white scales; inconspicuous dark greyish-blue markings appear where scales are dense enough as a submedial patch under midline and a postmedial spot on midline; off-white markings as a small notch subapically on costal margin and another opposite on inner margin. Hindwing silver grey. Subcostal brush absent. Abdomen dorsally uniform silver grey with

metallic blue iridescence; ventrally off-white, with tuft of long pale beige to dark-brown scales on each side of genitalia. Sclerotized hook arising from distinct sclerotized ring on the right side of tergum VII, large with pointed apex; minute sclerotized point on the left side. Genital flaps on sternum VIII, rounded, broad, and thin.

Male genitalia ($N = 1$) (Fig. 10). Uncus-like processes attached to tegumen, right process elongate and flattened on entire length, curved ventrally, apically pointed, about eight \times length of left process. Tegumen wide, heavily sclerotized, dorsoventrally flattened. Valvae symmetrical, with long and slender arms, enlarged apically, bent upward in the middle, adorned with setae arranged comb-like along dorsal margin, with three sclerotized spur-like setae of same length on each valva, minute and apically rounded on right valva, large and claw-like on left valva, being nine \times length of those on right valva. Phallus large, heavily sclerotized, slightly bent to the right, blunt tipped, with large bulbous base; vesica without spines or cornuti. Anellus with two lobes, thin, angled upward, both adorned with small setae until apex, left lobe bulbous apically.

Female ($N = 7$). Wingspan 8.0–9.4 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 11F). Papillae anales slightly longer than large. Apophyses thin and straight, with posterior apophyses very long, about three \times length of anterior apophyses. Ostium-bearing process heavily sclerotized, snail-shell shaped, with broad base. Ductus bursae long and of small girth. Corpus bursae oval and elongate, and with light scobination; signum absent. Inception of ductus seminalis very enlarged, cylindrical, situated behind of corpus bursae. Apical margin of sternum VII with no emargination medially.

Larval case ($N = 95$) (Fig. 2C). Cone-shaped structure, 5.0–6.0 mm in length, very small, decorated with dark brown and black bits of sand woven with silver silk filaments; uniform coloured; aperture of case width covered with a flat and bare operculum, unlike cone case type species where the aperture is often obscured by attached pebbles and frass, can be closed tightly by the larvae with its mandibles from the inside; each lateral side of aperture adorned with distinctive horns; case unadorned with pebbles, lid is clearly visible; background colour ranging from pale grey to slate grey.

Etymology: The name *H. wailua* is derived from the Wailua river on the island of Kauai where this species can be found.

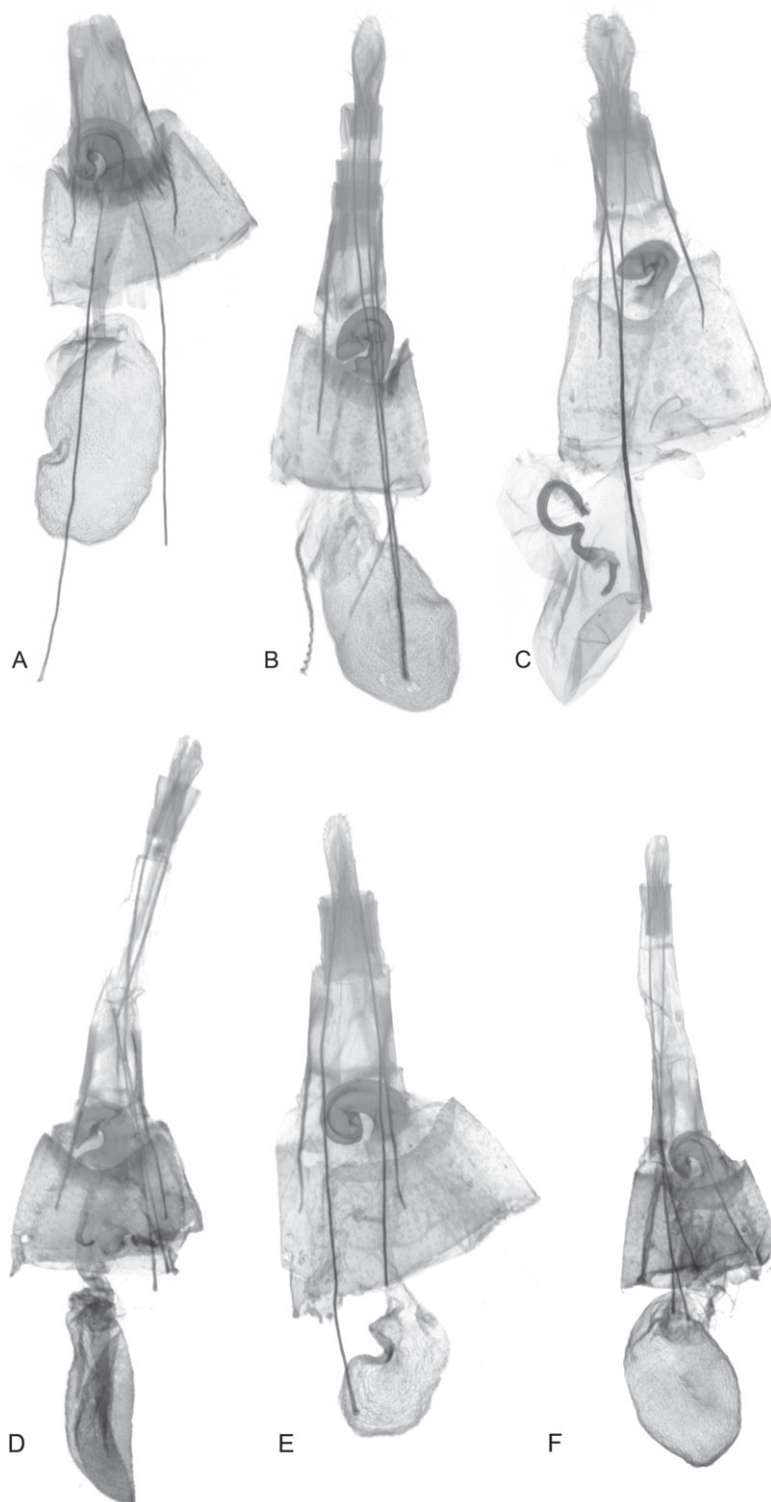


Figure 11. Female genitalia of *Hyposmocoma* spp., ventral aspect. A, *Hyposmocoma kahamanoa* sp. nov. (slide PS153); B, *Hyposmocoma uhauiole* sp. nov. (slide PS143); C, *Hyposmocoma kahaiao* sp. nov. (slide PS149); D, *Hyposmocoma kawaiikoi* sp. nov. (slide PS199); E, *Hyposmocoma kamakou* sp. nov. (slide PS166); F, *Hyposmocoma wailua* sp. nov. (slide PS201).

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in the Wailua river on the island of Kauai in February.

Distribution: Known only from the upper reaches of the Wailua river on the island of Kauai where it is presumed to be endemic.

Remarks: This aquatic species has the smallest cone-cased larva. Initially this cone case species was mistaken for a variation of the typical bugle-cased species, *H. eepawai*, we found in Kawaikoi stream on west Kauai. However, careful rearing and systematic analysis revealed that there are two different and distinctive cone case type species, *H. wailua* and *H. uhauiole*, in the Wailua river occurring together in large numbers on the same rocks. However, for some reason *H. wailua* is not also found in the Uhau'iole stream whereas both the cone-cased *H. uhauiole* and the burrito-cased *H. ipowainui* occur in both the Wailua and Uhau'iole streams. Although it is possible that our collecting has failed to discover *H. wailua* in Uhau'iole stream, we have made repeated trips and collected hundreds of larvae. It therefore now seems more likely that different aquatic species may have significantly different sensitivities to habitat conditions or water quality.

***HYPOSMOCOMA EEPAWAI* SCHMITZ & RUBINOFF
SP. NOV. (FIGS 12A, 14A, 15, 20A)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, Kawaikoi stream | N 22.13158°, W 159.62161° | elev[ation]. 3490 f[ee]t, 'bugle' case, II-24-09 | em[ergence]. IV-13-09, #DR09B7B | coll[ectors]. P[atrick]. Schmitz, D[aniel]. Rubinoff, M[ichael]. San Jose'; [2] 'HOLOTYPE | *Hypsmocoma* | eepawai | Schmitz and Rubinoff. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 18 ♂, 15 ♀, from Kauai Island, Hawaii, USA; 4 ♂, 3 ♀, with same data as holotype; 7 ♂, 1 ♀, with same data as holotype except date of emergence: 14.iv.2009 (2 ♂), 15.iv.2009 (2 ♂), 20.iv.2009 (3 ♂, 1 ♀); 7 ♂, 10 ♀, HI: Kauai, Alakai Swamp area, Kawaikoi stream at road, 'cone' case, V-18-05, em. 18.vi.2005 (2 ♂, one dissected PS144), 16.vi.2005 (4 ♂, 2 ♀), 19.vi.2005 (1 ♂, dissected PS156), 24.vi.2005 (1 ♀), 28.vi.2005 (1 ♀), 1.vii.2005 (5 ♀, one dissected PS179), 7.vii.2005 (1 ♀), #DR05E1, leg[it]. D. Rubinoff, W[ill]. Haines; 1 ♀ (dissected PS145). Deposited in BPBM, MHNG, UHIM, and USNM.

Diagnosis: Within the genus *Hypsmocoma*, *H. eepawai* is a mostly uniform greyish-blue colour that is somewhat similar in forewing pattern to *H.*

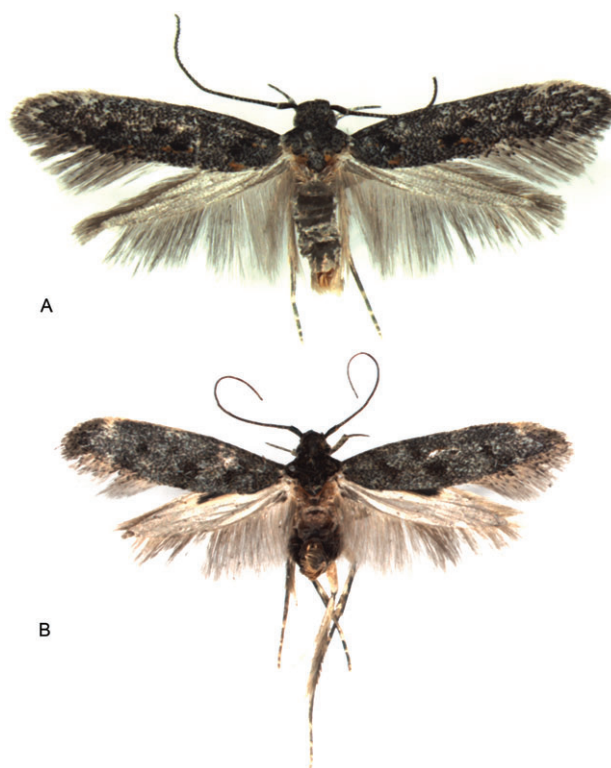


Figure 12. Holotypes of aquatic bugle and large burrito-case *Hypsmocoma* spp., adult males. A, *Hypsmocoma eepawai* sp. nov.; B, *Hypsmocoma ipowainui* sp. nov.

ipowainui sp. nov., *H. kaikuono* Schmitz & Rubinoff, 2008, and *H. kaupo* Schmitz & Rubinoff, 2008. However, it can be easily separated from these species by its smaller size, the absence of subcostal brush, and the differences in male and female genitalia.

Description: Male ($N = 16$) (Figs 12A, 15). Wingspan 10.4–10.6 mm (holotype: 10.6 mm). Head with greyish-blue white tipped scales. Haustellum with greyish blue, brown tipped scales. Maxillary palpus reduced. Labial palpus recurved with greyish-blue brown tipped scales, subapically white ring on second segment, and slender darkish brown third segment. Antenna flagellum darkish brown; scape with scales white tipped at the end; antennal pecten present with up to eight thin setae. Thorax greyish-blue; metascutellum greyish-beige. Foreleg coxa with off-white and greyish-blue brown tipped scales; femur, tibia, and tarsomeres mostly darkish brown with off-white ring at apex and middle of tibia, and apex of tarsomeres I–V. Midleg as foreleg, but also with ring of greyish-blue scales on tibia postmedially and extended off-white rings, spurs off-white. Hindleg as midleg. Forewing mostly greyish-blue with pale tipped scales, with very few scattered rusty scales; dark brown markings as a basal band, a pair of spots

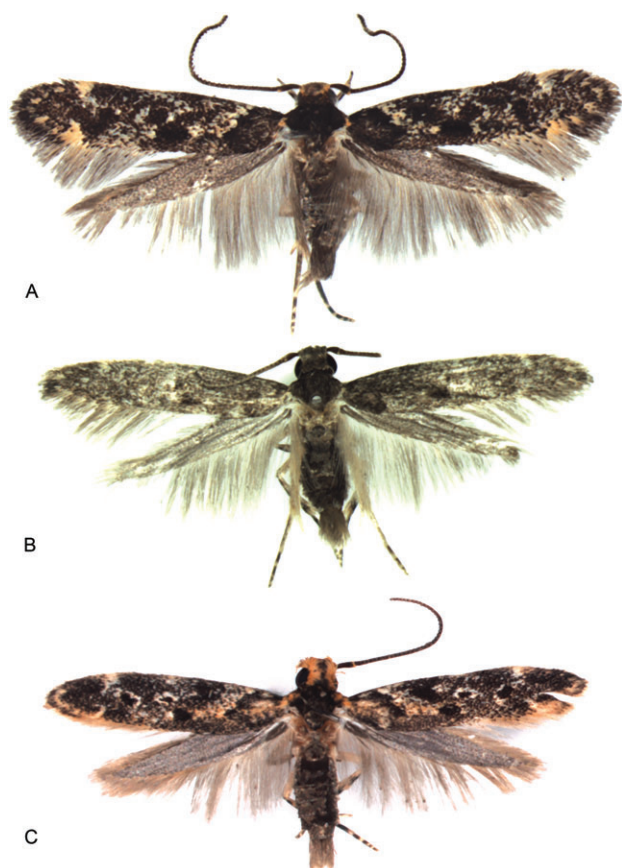


Figure 13. Holotypes of aquatic medium burrito-case *Hyposmocoma* spp., adult males. A, *Hyposmocoma aumakuawai* sp. nov.; B, *Hyposmocoma waihohonu* sp. nov.; C, *Hyposmocoma moopalikea* sp. nov.

medially, disconnected from each other along diagonal, and a more or less conspicuous small spot post-medially in midline; off-white markings as a small notch subapically on costal margin and another opposite on inner margin. Hindwing greyish brown. Subcostal brush absent. Abdomen dorsally uniform shiny grey; ventrally off-white, with tuft of long pale beige scales on each side of genitalia. Sclerotized hook arising from distinct sclerotized ring on the right side of VII abdominal tergum, large with blunt apex; minute sclerotized point on the left side. Genital flaps on VIII abdominal sternum, rounded, broad, and thin.

Male genitalia ($N = 2$) (Fig. 15). Uncus-like processes attached to tegumen, right process elongate and flattened on entire length, curved ventrally, apically pointed, about $6.5 \times$ length of left process. Tegumen wide, heavily sclerotized, dorsoventrally flattened. Valvae symmetrical, with long and slender arms, slightly enlarged apically, bent upward in the middle, adorned with setae arranged comb-like along

dorsal margin, with two sclerotized spur-like setae of same length on each valva, minute and apically rounded on right valva, large and claw-like on left valva, being $6 \times$ length of those on right valva. Phallus large, heavily sclerotized, slightly bent to the right, blunt tipped, with large bulbous base; vesica without spines or cornuti. Anellus with two lobes, thin, angled upward, both adorned with small setae until apex, left lobe bulbous apically.

Female ($N = 14$). Wingspan 10.1–11.7 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 20A). Papillae anales slightly longer than large. Apophyses thin and straight, with posterior apophyses very long about $3 \times$ length of anterior apophyses. Ostium-bearing process heavily sclerotized, atrophied, with broad base. Ductus bursae long and of small girth. Corpus bursae oval and elongate, with light scobination; signum absent. Inception of ductus seminalis very enlarged, cylindrical, situated behind of corpus bursae. Apical margin of sternum VII with no emargination medially.

Larval case ($N = 82$) (Fig. 14A). Bugle-shaped structure, 4.0–6.5 mm in length, small and triangular, decorated with beige, brown, and black bits of sand woven densely with silk filaments; bicoloured, underside shiny grey, darker above; aperture of case covered with a flat and bare operculum, that can be closed tightly by the larvae with its mandibles from the inside; case background colour dark grey.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks of Kawaikoi stream on the island of Kauai in February and May.

Distribution: Known only from the island of Kauai where the Kawaikoi stream drains the north-western plateau of the Alaka'i swamp. We have found it nowhere else and therefore presume it to be endemic to this drainage.

Etymology: The name *H. eepawai*, from the Hawaiian, 'ēpa, a supernatural being in Hawaiian mythology with a strange shape, refers to the bugle shape of the larval case of this species, and, wai, water, refers to its aquatic lifestyle.

Remarks: Remarkably, the island of Kauai supports three endemic species of aquatic cones, *H. kawaikoi*, *H. uhauiole*, and *H. wailua*, whereas there is only a single aquatic bugle case type, *H. eepawai*, found only in the Alaka'i swamp on west Kauai. Not only are these two case types independent lineages, as confirmed by genetic analysis (Rubinoff & Schmitz,

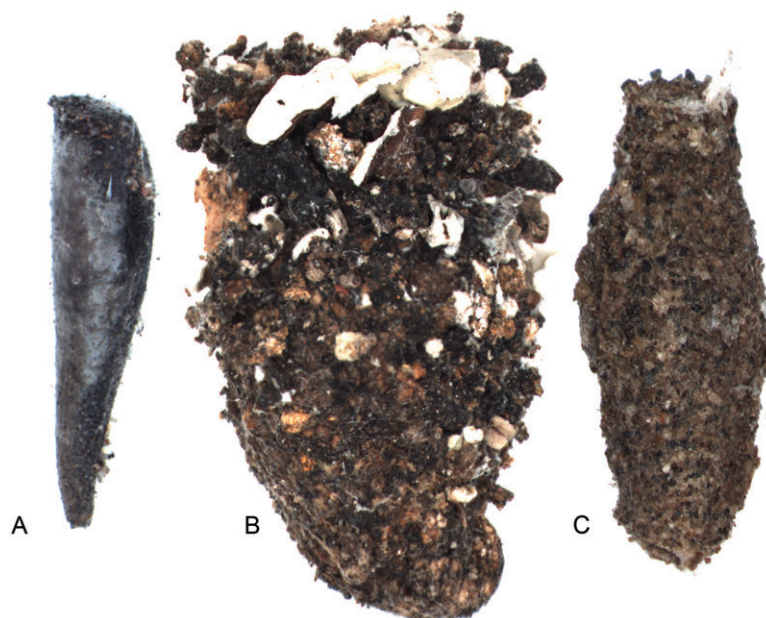


Figure 14. Case types of aquatic *Hyposmocoma* spp., larvae. A, *Hyposmocoma eepawai* sp. nov., lateral aspect; B, *Hyposmocoma ipowainui* sp. nov., dorsal aspect; C, *Hyposmocoma aumakuawai* sp. nov., dorsal aspect.

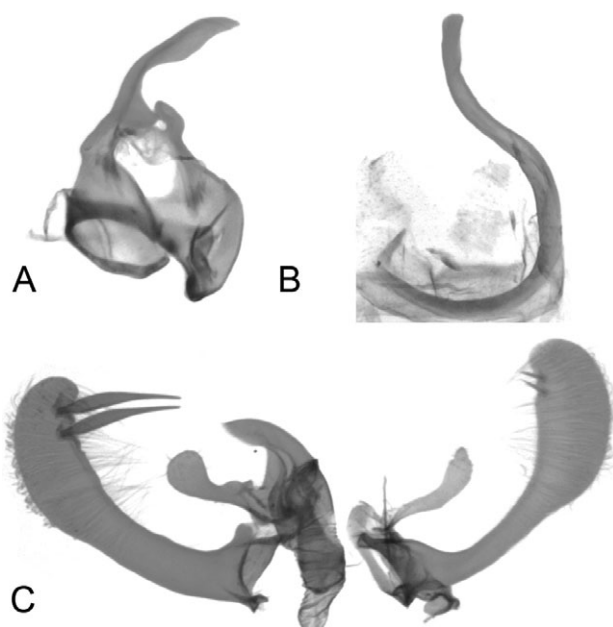


Figure 15. Male genitalia of *Hyposmocoma eepawai* sp. nov. from specimen on slide PS156. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

2010), but also the similar case types reveal very localized speciation across this oldest of the current high Islands. It is interesting to note that like many other *Hyposmocoma* species, whereas adults of *H. eepawai* and *H. cinerosparsa* Walsingham, 1907, both

occurring on Kauai, are externally completely different, their male and female genitalia are almost identical.

***HYPSMOCOMA IPOWAINUI* SCHMITZ & RUBINOFF
SP. NOV. (FIGS 12B, 14B, 16, 20B)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, Uhau'iole Stream | 'burrito' case, VIII-8-[20]07 | em[ergence]. VIII-11-[20]07, #DR07H1B | leg[it]. D[aniel]. Rubinoff, W[ill]. Haines'; [2] 'HOLOTYPE | *Hyposmocoma* | ipowainui | Schmitz and Rubinoff'. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 10 ♂, 13 ♀, from Kauai Island, Hawaii, USA; 1 ♂, with same data as holotype; 3 ♂, 5 ♀, with same data as holotype except date of emergence: 19.viii.2007 (1 ♀), 26.viii.2007 (1 ♀), 11.ix.2007 (1 ♂, dissected PS146), 27.ix.2007 (1 ♀), 3.i.2008 (1 ♂); 1 ♂, 2 ♀, HI: Kauai Island, Uhau'iole Stream, amongst rocks, 8.viii.2007, Haines, Rubinoff, coll[ectors].; 3 ♂ (one dissected, PS112), 5 ♀ (one dissected, PS147), HI: Kauai co. N. fork Wailua R[i]v[e]r. Blue Hole Tr[ai]ll. H[ea]d. 'burrito', 27.ii.2004, Em[el]rg[ed]. 3/12.v.2004, Rubinoff, coll[ector].; 1 ♀, HI: Kauai, Alakai Swamp area, Kawaikoi stream, 'burrito' case, 3.vi.2004, em. 19.vii.2004, leg. D. Rubinoff; 1 ♀, HI: Kauai, Alakai Swamp area, Kawaikoi stream, 'burrito' case, 18.v.2005, em[ergence]. 16.vi.2005, #DR05E2, leg. D. Rubinoff, W. Haines *et al.*; 1 ♀, HI: Kauai, Kawaikoi stream, N 22.13158°, W 159.62161°, elev[ation]. 3490 f[ee]t, 'burrito' case, 24.ii.2009, em.

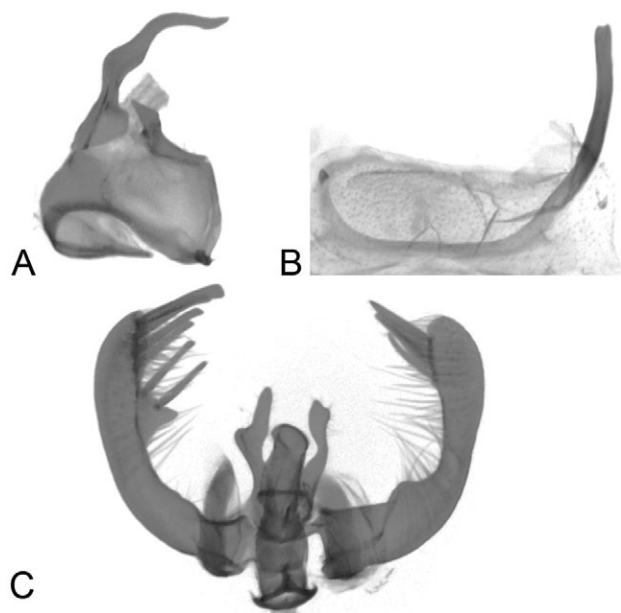


Figure 16. Male genitalia of *Hyposmocoma ipowainui* sp. nov. from specimen on slide PS146. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

23.iii.2009, #DR09B7C, coll. P[atrack]. Schmitz, D. Rubinoff, M[ichael]. San Jose; 3 ♂, HI: Kauai, Keahua stream, N 22.07143°, W 159.41765°, elev. 602 ft, 'burrito' case, 23.ii.2004, em. 12.iii.2009, coll. P. Schmitz, D. Rubinoff, M. San Jose. Deposited in BPBM, MHNG, UHIM, and USNM.

Diagnosis: In the genus *Hyposmocoma*, *H. ipowainui* is a relatively large species closely related to *Hyposmocoma kaikuono* Schmitz & Rubinoff, 2008 endemic to the island of Molokai, *Hyposmocoma kapakai* Schmitz & Rubinoff, 2008 endemic to the island of Oahu, *Hyposmocoma kaupo* Schmitz & Rubinoff, 2008 endemic to the island of Maui, and *Hyposmocoma montivolans* (Butler, 1882) endemic to the island of Oahu. Based only on wing pattern, *H. ipowainui* can be separated from *H. kapakai* and *H. montivolans* by the forewing ground colour being greyish blue and not olive green. It differs also in male genitalia from *H. kapakai* and *H. montivolans* by having a triangular projection on left valva like the other species mentioned, from *H. kaikuono* by having six sclerotized spur-like setae on each valva, two of them on the triangular projection, from *H. kaupo* by having a broad sclerotized ring on abdominal segment VII, and from *H. kaikuono*, *H. kapakai*, *H. kaupo*, and *H. montivolans* by having a straight, thick, and blunt sclerotized hook, not enlarged apically.

Description: Male ($N = 8$) (Figs 12B, 16). Wingspan 11.8–14.5 mm (holotype: 13.3 mm). Head with greyish-blue white-tipped scales converging toward

midline on occiput. Haustellum with greyish-blue brown-tipped scales. Maxillary palpus reduced. Labial palpus recurved with greyish-blue brown-tipped scales, subapically white ring on second segment, and slender dark-brown third segment. Antenna flagellum darkish brown; scape with scales white tipped at the end; antennal pecten present with up to eight thin setae. Thorax mostly greyish blue; dark brown at collar and at apex medially, with yellowish-orange scales laterally, more or less conspicuous and forming sometimes small spots; apex of tegula and outer margin of metathorax dark brown; metascutellum greyish beige. Foreleg coxa with off-white and greyish-blue brown-tipped scales; femur, tibia, and tarsomeres mostly dark brown with off-white ring at middle and apex of tibia, and apex of tarsomeres I–V. Midleg as foreleg, but also with ring of greyish-blue scales on tibia postmedially and extended off-white rings, spurs off-white. Hindleg as midleg. Forewing mostly greyish-blue with pale-tipped scales; off-white scales at jointure of wing; dark-brown markings as a basal band, a small baso-costal spot not reaching dorsal margin, a medium size patch postbasally (slightly below midline), a submedial patch above midline, a larger oval submedially along posterior margin without reaching it, a medium size patch medially in middle of wing just above submedial oval, and a pair of medium patches, sometimes joined, situated postmedially, the patch below reaching inner margin; small off-white spots occurring at half and three-quarters along dorsal margin, with sometimes slightly off-white markings as small dots around dark-brown markings; fringe off-white to greyish beige with darker-tipped scales. Hindwing greyish brown with greyish-beige fringe. Subcostal brush conspicuous, on dorsal surface on anterior margin, dark grey extending half the length of hindwing (see Fig. 12B). Abdomen dorsally uniform shiny grey; ventrally off-white, with tuft of long pale beige scales on each side of genitalia. Sclerotized hook arising from distinct sclerotized ring on the right side of tergum VII, elongate, slightly curved, narrowing apically to blunt apex; minute sclerotized point on the left side; sternum VII with triangular fold in the middle pointing perpendicularly. Genital flaps on sternum VIII, rounded, broad, and thin.

Male genitalia ($N = 2$) (Fig. 16). Uncus-like processes with right process elongate, curved ventrally, apically pointed, about four \times longer than reduced left process. Tegumen wide, heavily sclerotized, dorsoventrally flattened, ventral connection broad. Valvae asymmetrical, with long and slender arms adorned with dense setae arranged comb-like along dorsal margin, broadened distally, with six prominent, uniformly spaced, sclerotized spur-like setae, sequentially longer distally, setae thinner and shorter,

arranged more densely on right valva, left valva with subapical triangular projection adorned with two spur-like setae. Phallus slightly bent to the right at about two-thirds of length, stout, blunt tipped, heavily sclerotized, bulbous at base. Anellus with asymmetrical lobes, left lobe with broad bulbous projection at middle, then terminating in short point, right lobe delicate and slightly curved, bulbous at end, both adorned with small setae, two to three very long setae on apex, two \times length of phallus.

Female ($N = 12$). Wingspan 12.6–16.0 mm. Frenulum with three acanthae. Antenna slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 2$) (Fig. 20B). Papillae anales short, lightly sclerotized and setose, slightly longer than wide, pointed lateroapically. Posterior apophyses very slender and straight, about five \times length of papillae anales. Anterior apophyses slightly broader and about one-third \times length of posterior apophyses. Ostium-bearing process heavily sclerotized, externally protruding, question-marked shaped, broad at base with sickle-shaped apex. Ductus bursae short, of medium girth. Inception of ductus seminalis large, at about one-third length of corpus bursae, situated behind of corpus bursae. Apical margin of sternum VII with slight broad emargination medially. Corpus bursae oval and elongate, with light scobination, lightly sclerotized from about middle to pointed proximal end; signum absent.

Larva cases ($N = 83$) (Fig. 14B). Burrito-shaped structure, 6.0–9.0 mm long, in reference to the shape of a type of Mexican food that consists of a flour tortilla wrapped around a filling, large and rounded with a curved pointed distal end, decorated with bits of sand, pebbles, and lichens entangled in silk filaments. Case background colour ranges from grey to brown.

Etymology: The name *H. ipowainui*, from the Hawaiian *ipo*, lover, *wai*, water, and *nui*, large, refers to its aquatic lifestyle and the relatively large size of the species.

Biology: All adults were reared from amphibious case-making larvae. Larvae were collected during the day in February, April, May, and August on rocks in streams of the island of Kauai. The adults of this species are relatively large and easily observed running, courting, and mating in broad daylight on emergent rocks in the streams where they occur. Larvae of this species have frequently been observed crawling underwater, deep in the middle of streams and using the silk 'safety-line' to reattach themselves to the underwater substrate when dislodged.

Distribution: Presumed to be endemic to the streams and rivers of the Hawaiian island of Kauai.

Remarks: This aquatic burrito species is amongst the largest on any of the islands. In remarkable contrast to the localized speciation of the cone and bugle species on Kauai, *H. ipowainui* is found across Kauai and the ranges of the other species and has apparently not speciated along the same geographical boundaries as the cone lineage. Further research into this phylogeographical discontinuity on Kauai and why it does not affect this species is warranted. This species can be abundant and smaller larvae may be mistaken for the smaller burrito-cased species *Hyposmocoma aumakuawai*, although the adult moths are clearly distinct, and experience with the larvae reveals differences in the cases.

HYPOSMOCOMA AUMAKUAWAI SCHMITZ & RUBINOFF
SP. NOV. (FIGS 13A, 14C, 17, 20C)

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Kauai, Kawaikoi stream | N 22.13158°, W 159.62161° | elev[ation]. 3490 f[ee]t, 'burrito' case, II-24-[20]09 | em[ergence]. IV-13-[20]09, #DR09B7D | coll[ectors]. P[atrick]. Schmitz, D[aniel]. Rubinoff, M[ichael]. San Jose'; [2] 'HOLOTYPE | *Hyposmocoma* | *aumakuawai* | Schmitz and Rubinoff'. Specimen in

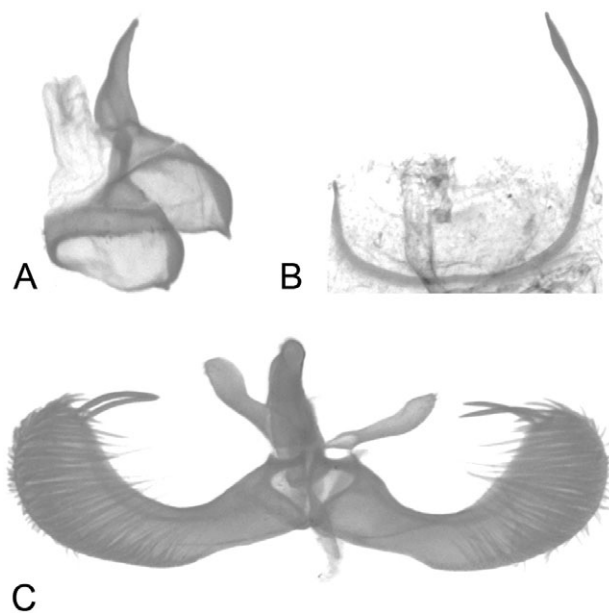


Figure 17. Male genitalia of *Hyposmocoma aumakuawai* sp. nov. from specimen on slide PS205. A, tegumen, ventral aspect; B, sclerotized hook on abdominal segment VII, ventral aspect; C, valvae with phallus, ventral aspect.

good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 7 ♂, 5 ♀, from Kauai Island, Hawaii, USA; 2 ♂, 1 ♀, with same data as holotype; 5 ♂, 4 ♀, with same data as holotype except date of emergence: 9.iii.2009 (2 ♂), 20.iii.2009 (1 ♂, 1 ♀, dissected PS203), 25.iii.2009 (2 ♀), 26.iii.2009 (1 ♂, 1 ♀) 6.iv.2009 (1 ♂, dissected PS202). Deposited in UHIM and USNM.

Diagnosis: Amongst the species of *Hypsmocoma*, *H. aumakuawai* is very similar to *Hypsmocoma moopalikea* sp. nov. and *Hypsmocoma parda* (Butler, 1881), both endemic to the island of Maui, in forewing pattern, but it differs in males by the presence of a sclerotized hook on abdominal segment VII.

Description: Male ($N = 8$) (Figs 13A, 17). Wingspan 9.1–11.2 mm (holotype: 9.7 mm). Head mostly dark brown becoming orange on vertex and frons with tuft of orange scales around eye. Haustellum with off-white scales. Maxillary palpus reduced. Recurved labial palpus mostly dark brown dorsally and off-white ventrally, with off-white to orange ring on second segment apically. Antennal flagellum dark brown; scape dark brown with orange ring apically, antennal pecten present with up to 11 thin setae. Thorax, tegula, and metascutellum dark brown. Foreleg dark brown with orange ring at middle and apex of tibia, and beige rings at apex of tarsomeres I–II. Midleg as foreleg, spurs beige. Hindleg as midleg, but ground colour more silver grey. Forewing with dark brown to dark grey background with scattered off-white blue tinge scales; dark-brown markings more or less conspicuous as pair of spots medially (sometimes fused), disconnected from each other along diagonal, and a small spot postmedially in midline; beige to orange markings as a spot at the joint of the wing, a notch subapically on costal margin and another opposite on inner margin, and as a line of tiny spots along termen. Hindwing uniformly dark grey. Subcostal brush absent. Abdomen dorsally dark grey; ventrally off-white, with tuft of long dark-grey scales on each side of genitalia. Sclerotized hook thin with pointed apex arising from distinct sclerotized ring on the right side of tergum VII, minute sclerotized point on the left side. Genital flaps very large, membranous, rounded, broad and thin.

Male genitalia ($N = 1$) (Fig. 17). Uncus-like processes with right process slightly curved downwards, dorsoventrally flattened, about four \times length of left stout process. Tegumen wide, heavily sclerotized, dorsoventrally flattened. Valvae symmetrical, spoon-shaped with short arms broader distally, slightly upcurved, adorned with dense setae arranged comb-like along dorsal margin, with two thin sclerotized

spur-like setae of same length on each valva. Phallus heavily sclerotized, bulbous about middle, slightly angled downwards at apex; vesica without spines or cornuti. Anellus with two symmetrical lobes, thin with bulbous apex, both adorned with small setae, with two or more very long setae on apex.

Female ($N = 5$). Wingspan 9.6–11.2 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 20C). Papillae anales slightly longer than large. Apophyses thin and straight, with posterior apophyses long about three \times length of anterior apophyses. Ostium-bearing process heavily sclerotized, snail-shell shaped, curved to the left, with broad base. Ductus bursae long and of small girth. Corpus bursae oval and elongate, and with light scobination; two signa, one on each side of corpus at about one quarter of length from apex, as two little patches adorned uniformly with spines. Inception of ductus seminalis very enlarged, cylindrical, situated behind of corpus bursae. Apical margin of sternum VII with no emargination medially.

Larval case ($N = 44$) (Fig. 14C). Burrito-shaped structure, 5.5–8.5 mm in length, medium sized and rounded without a curved pointed distal end, decorated with grey and brown bits of sand and pebbles, entangled in silk filaments. Case background colour ranges from grey to brown.

Etymology: The name *H. aumakuawai*, from the Hawaiian, 'au makua, a deified ancestor or spirit who assumes a shape of an animal, refers to the caterpillar of this species, and wai, water, refers to its aquatic lifestyle.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in the Kawaikoi stream on the island of Kauai in February.

Distribution: Known only from the island of Kauai where it is presumed to be endemic.

Remarks: Because the larval case of this species looks very similar to *H. ipowainui*, it may be that *H. aumakuawai* occurs in eastern Kauai as well but has gone unnoticed despite our extensive collections. However, at this juncture it is more prudent for us to assume that this species is endemic to western Kauai as are the bugle species *H. eepawai* and the cone species *H. kawaikoi*. This is particularly appropriate because we have reared many dozens of burrito-cased larvae from eastern Kauai and *H. aumakuawai* has not appeared there yet. The reasons for the extremely

local endemism of this burrito case but not *H. ipowainui* bear further study.

***HYPOSMOCOMA WAIHOHONU* SCHMITZ & RUBINOFF
SP. NOV. (FIGS 13B, 18, 20D)**

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: West Maui | Maui Land and Pineapple | Honolulu Stream, elev[ation]. 900 m | 'burrito' case, I-6-[20]06, em[er]gence]. II-20-[20]06, #DR06A8 | leg[it]. D[ani]el. Rubinoff'; [2] 'HOLOTYPE | Hyposmocoma | wai-honu | Schmitz and Rubinoff'. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 9 ♂, 11 ♀, from Maui Island, Hawaii, USA; 2 ♂, 4 ♀ (one dissected, PS151), same data as holotype; 3 ♂, 3 ♀, same data as holotype except date of emergence: 11.ii.2006 (2 ♂, one dissected PS150), 17.ii.2006 (2 ♀), 21.ii.2006 (1 ♀), 3.iii.2006 (1 ♂, dissected PS158); 4 ♂, 2 ♀, HI: W[est]. Maui Isl[and]., Iao V[all]y. St[rea]m., 'burrito', 11.ix.2004, Em[er]g[ence]: 1.x.2004 (1 ♂), 6.x.2004 (1 ♀), 10.x.2004 (1 ♂), 18.x.2004 (1 ♀), 28.x.2004 (1 ♂), 15.xi.2004 (1 ♂), Rubinoff, coll[ector]; 2 ♀, HI: W[est]. Maui, Waiehu stream, 'burrito', 22/25.ix.2008, em[er]gence]. 3.xi.2008, #DR08I3B, coll. C[ynth]ia. King. Deposited in BPBM, UHIM, and USNM.

Diagnosis: *Hyposmocoma waihohonu* is a relatively small mostly uniform dark brown to dark grey species. Amongst the species of *Hyposmocoma*, *H.*

waihohonu can be easily separated by the combination of its size and coloration.

Description: Male ($N = 9$) (Figs 13B, 18). Wingspan 8.4–9.7 mm (holotype: 8.6 mm). Head mostly dark brown becoming dark grey on vertex and off-white on frons. Haustellum with off-white scales. Maxillary palpus reduced. Recurved labial palpus mostly dark brown dorsally and off-white ventrally, with off-white ring on second segment apically. Antennal flagellum dark brown; scape dark brown with off-white ring apically, antennal pecten present with up to eight thin setae. Thorax, tegula, and metascutellum dark brown. Foreleg coxa off-white; femur dark brown; tibia and tarsomeres dark brown with off-white ring at middle and apex of tibia, and apex of tarsomeres I–V. Midleg as foreleg, spurs off-white. Hindleg as midleg, but ground colour more silver grey. Forewing with dark brown to dark grey background, with more or less conspicuous dark brown markings as pair of spots medially (often fused in darker specimens), disconnected from each other along diagonal, and a small spot postmedially in midline; indistinct off-white markings as a small notch subapically on costal margin and another opposite on inner margin. Hindwing uniformly dark grey with fringe greyish brown. Subcostal brush absent. Abdomen dorsally dark brown to dark grey; ventrally off-white, with tuft of long dark-grey scales on each side of genitalia. Sclerotized hook absent. Genital flaps very large, membranous, rounded, broad and thin.

Male genitalia ($N = 2$) (Fig. 18). As for *H. aumakuawai*.

Female ($N = 9$). Wingspan 8.9–9.4 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 20D). As for *H. aumakuawai*.

Larval case ($N = 86$). Burrito-shaped structure, 4.0–5.5 mm in length, as *H. aumakuawai*.

Etymology: The name *H. waihohonu*, from the Hawaiian, *wai*, water, refers to its aquatic lifestyle, and *hohonu*, deep, refers to the habit of this species to frequent deep, central stream channels.

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in the streams on the western volcano of the island of Maui in January, September, and November. This species was frequently observed in deep water in the central channel of the streams in which it occurs, although, like all aquatic species, it is frequently found resting above the water line. This may be in part a function of our relative ease in finding

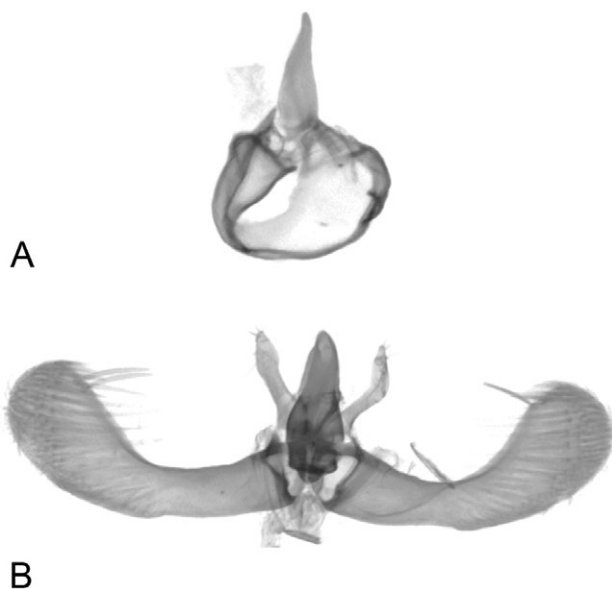


Figure 18. Male genitalia of *Hyposmocoma waihohonu* sp. nov. from specimen on slide PS158. A, tegumen, ventral aspect; B, valvae with phallus, ventral aspect.

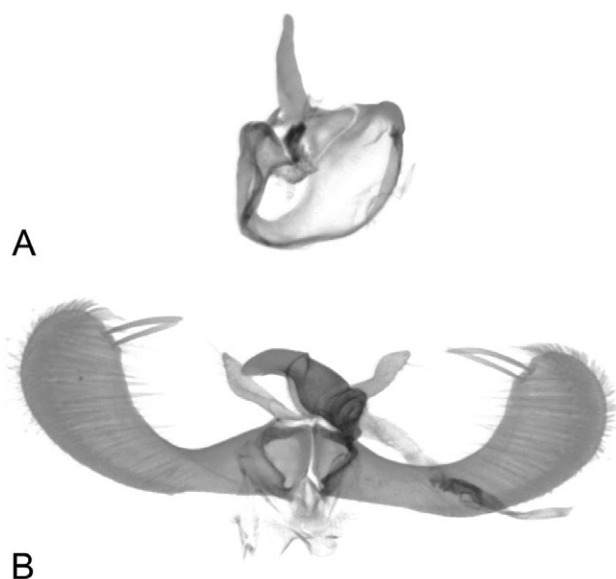


Figure 19. Male genitalia of *Hyposmocoma moopalikea* sp. nov. from specimen on slide PS170. A, tegumen, ventral aspect; B, valvae with phallus, ventral aspect.

larvae out of the water rather than when submerged and under rocks in the middle of fast flowing streams.

Distribution: Known only from the Hawaiian Island of Maui where it is presumed to be endemic of the streams of west Maui (Honolua, Iao, and Waiehu streams).

Remarks: Parasitoids ($N = 10$ from #DR09I3B) were reared from some larvae and have been identified as belonging to the genus *Euderus* of the Eulophidae (Hymenoptera). This species appears to be the sister taxon to the aquatic burrito species, *H. moopalikea*, restricted to the south side of east Maui.

HYPSMOCOMA MOOPALIKEA SCHMITZ & RUBINOFF
SP. NOV. (FIGS 13C, 19, 20E)

Material examined: HOLOTYPE ♂: [1] 'H[AWAI]I: Maui, Haleakala N[at]ional.P[ark]. | Palikea stream, N Delta camp | 'burrito' case, on rocks, I-15-[20]04 | em[ergence]. II-4-04 | coll[ector]. D[aniel]. Rubinoff; [2] 'HOLOTYPE | Hyposmocoma | moopalikea | Schmitz and Rubinoff. Specimen in good condition except for broken antennae. Deposited in the UHIM.

PARATYPES: 3 ♂, 2 ♀, from Maui Island, Hawaii, USA, with same data as holotype except date of emergence: 4.ii.2004 (1 ♂), 16.ii.2004 (1 ♂), 19.ii.2004 (1 ♀), 25.ii.2004 (1 ♀), 7.iii.2004 (1 ♂). Deposited in UHIM.

Diagnosis: *Hyposmocoma moopalikea* is most similar in forewing markings to *H. aumakuawai* sp. nov., and *H. parda* (Butler, 1881), but it differs from these species in having on the forewing scattered yellowish-orange scales and a conspicuous pair of spots outlined by off-white scales. In addition, it differs from *H. aumakuawai* in the absence of a sclerotized hook on abdominal segment VII.

Description: Male ($N = 4$) (Figs 13C, 19). Wingspan 10.3–11.2 mm (holotype: 10.5 mm). Head mostly adorned with grey-tipped yellowish-orange scales becoming off-white on frons. Haustellum with off-white and dark-brown scales. Maxillary palpus reduced. Recurved labial palpus mostly dark brown dorsally and off-white ventrally, with dark brown ring on first segment apically. Antennal flagellum dark brown; scape dark brown with rusty ring apically, antennal pecten present with five to seven thin setae. Thorax mostly dark brown, with yellowish-orange scales on tegula; metathorax grey; metascutellum greyish-beige. Foreleg coxa off-white; femur dark brown; tibia and tarsomeres dark brown with off-white ring at middle and apex of tibia, and apex of tarsomeres I, II, and V. Midleg as foreleg, spurs off-white. Hindleg as midleg, but ground colour more greyish beige. Forewing mostly dark brown with some scattered off-white scales becoming yellowish-orange at base of forewing along midline and on termen, with conspicuous dark brown markings outlined by off-white scales as pair of spots medially, disconnected from each other along diagonal, and a small spot postmedially in midline; off-white markings as a small notch subapically on costal margin and another opposite on inner margin. Hindwing uniformly grey with greyish-beige fringe. Subcostal brush absent. Abdomen dorsally dark brown; ventrally off-white, with tuft of long greyish-brown scales on each side of genitalia. Sclerotized hook absent. Genital flaps very large, membranous, rounded, broad and thin.

Male genitalia ($N = 1$) (Fig. 19). As for *H. aumakuawai*.

Female ($N = 2$). Wingspan 11.7–11.9 mm. Frenulum with three acanthae. Antennae slightly thinner than that of male, yellowish-orange scales restricted at jointure of forewing. Otherwise externally like males.

Female genitalia ($N = 1$) (Fig. 20E). As for *H. aumakuawai*.

Larval case ($N = 9$). Burrito-shaped structure, 5.5–7.0 mm in length, as *H. aumakuawai*.

Etymology: The name *H. moopalikea*, from the Hawaiian, *moo*, water spirit, refers to its aquatic lifestyle, and *palikea* refers to the name of the reserve and stream where this species was found.

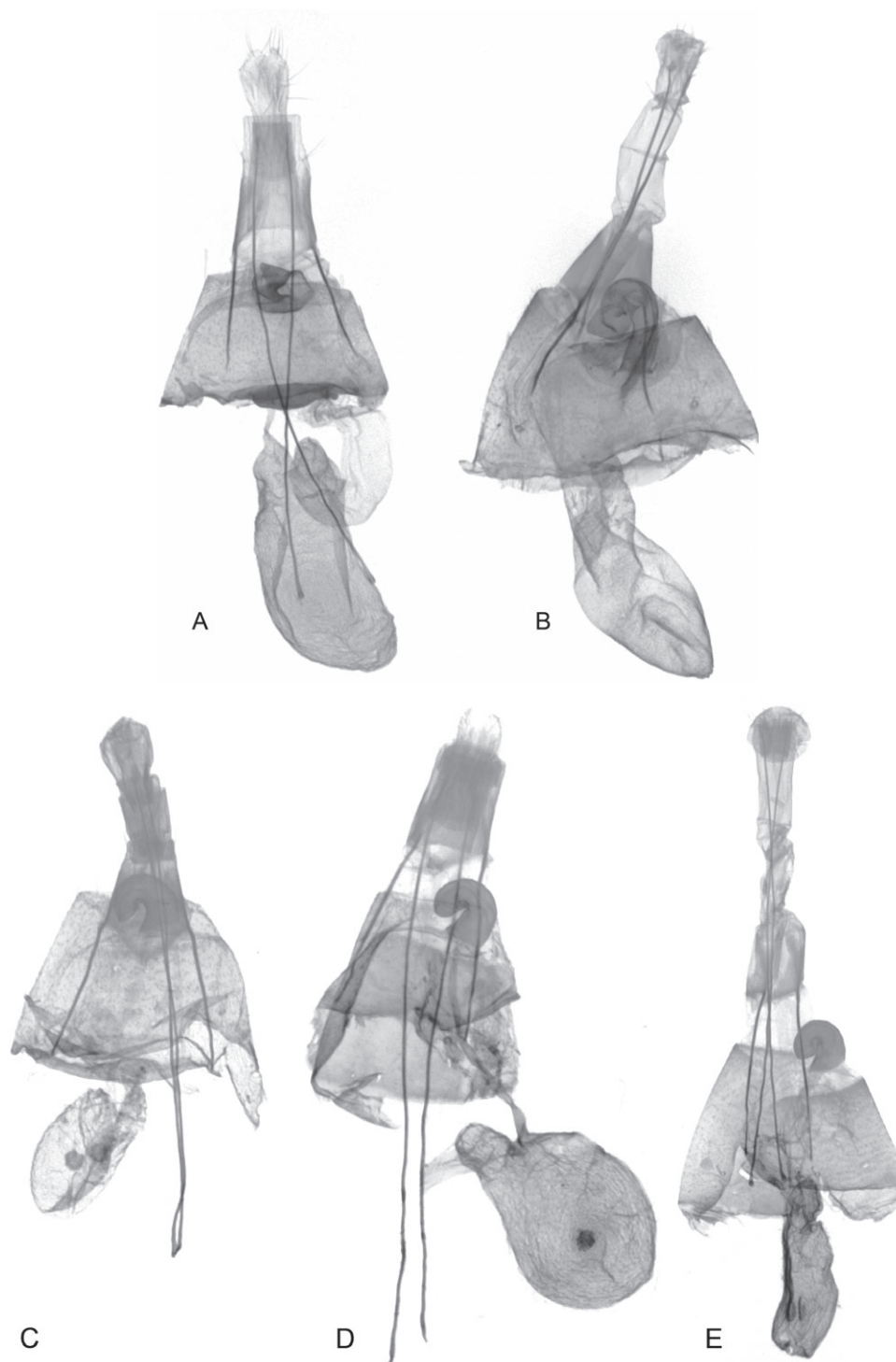


Figure 20. Female genitalia of *Hyposmocoma* spp., ventral aspect. A, *Hyposmocoma eepawai* sp. nov. (slide PS179); B, *Hyposmocoma ipowainui* sp. nov. (slide PS147); C, *Hyposmocoma aumakuawai* sp. nov. (slide PS203); D, *Hyposmocoma waihohonu* sp. nov. (slide PS169); E, *Hyposmocoma moopalikea* sp. nov. (slide PS171).

Biology: Adults were reared from amphibious case-making larvae. Case-bearing larvae were collected during the day on rocks in the Palikea stream on the island of Maui in January, but also seen in late spring, and are likely to be present year-round. Adult moths were observed flying and crawling very quickly across emergent rocks and flying between them in the middle of the stream during the mid and late afternoon. Blacklight traps placed next to the Palikea stream that same night attracted no adults of *H. moopalikea*, suggesting that they are diurnal in this wet, cool, montane rainforest environment.

Distribution: Known only from the Palikea stream in the Kipahulu valley of east Maui where it is presumed to be endemic.

Remarks: This species appears to occur in allopatry from any other aquatic species. It is rarely abundant, and despite extensive searching, we were unable to collect larvae in large numbers as easily as other species on other islands. As this area represents the most pristine of any area where we collected aquatic species, we doubt that this rarity is a function of severe habitat alteration.

DISCUSSION

UNDERWATER BREATHING STRATEGY

Through laboratory and field observations it is clear that *Hypsmocoma* larvae do not need to return to the surface quickly (or for days), when grazing algae on submerged rocks in fast flowing streams. As the larvae do not bear specialized morphological structures in order to breathe underwater, such as tracheal gills, closed spiracles, and hydrofuge hair systems, for example, and they do not store an air bubble inside the case, it seems that they breathe by direct diffusion through their hydrophilic skin. This is supported in that they are always restricted to fast-flowing streams where high dissolved oxygen concentrations are typical. When placed in still water, the larvae die in a matter of hours.

COMPLEX SPECIATION AND ENDEMISM PATTERNS

The phylogenetic analysis revealed a topology (Fig. 21) that was congruent with the relationships inferred from a much larger dataset that incorporated 216 individuals from 89 taxa, including many terrestrial species of *Hypsmocoma* (Rubinoff & Schmitz, 2010). That study confirmed the independent origins of several of the aquatic case lineages, but offered limited taxonomic information. The current phylogeny is not meant to supplant the evolutionary relationships established in the prior, larger analysis, but

rather to demonstrate for the first time, the relationships of the newly described species in their respective species groups (but the apparently close relationships between the different aquatic case types are in many instances separated by multiple terrestrial lineages not included in the present study).

The purpose of the phylogeny (Fig. 21), rather than addressing broad evolutionary patterns across the genus, was to provide a convenient framework focused on the species described in the present study demonstrating localized relationships between the newly described species and their closest sister taxa in a phylogenetic framework. Thus, for the current study, we analysed a specific group of taxa, including the new aquatic species and only their closest terrestrial sister taxa, as necessary, to demonstrate relationships between and within each monophyletic aquatic species group. These results are congruent with the larger analysis (Rubinoff & Schmitz, 2010) and demonstrate four distinct, monophyletic aquatic species case types, including the cone, bugle, medium burrito, and large burrito cased lineages. Each lineage contains between two and nine species, some of which are terrestrial (e.g. *H. laysanensis*, *H. saccophora*, and *Hypsmocoma* sp. 1 in the cone lineage, *Hypsmocoma* sp. 2 in the bugle lineage, and *H. kaupo*, *H. kaikuono*, and *H. kapakai* in the large burrito lineage). Although the current phylogeny does not contain enough taxa to demonstrate the polarity of the aquatic/terrestrial ecology in the genus, this was addressed in a previous study (see Rubinoff & Schmitz, 2010).

Aquatic cone bearers speciated on Kauai but apparently not on other islands, although terrestrial cone bearers also occur, allopatrically, on Oahu and Maui (Fig. 21). Interestingly, the three different morphologies of case types are represented on Kauai (Fig. 2). The three aquatic cone-cased species, *H. kawaikoi*, *H. uhauiole*, and *H. wailua* are restricted to west or east Kauai, the bugle-cased species, *H. eepawai*, and the medium burrito-cased species, *H. aumakuawai*, are restricted to west Kauai, yet the large burrito-cased species, *H. ipowainui*, is the one island-wide species on Kauai. This discordant and unpredictable phylogeography amongst aquatic lineages suggests dispersal rather than vicariance as the mode of speciation. In particular, species-specific factors and not broader hydrological history may be more important in supporting speciation events in these groups, at least on Kauai. Further phylogenetic study will be important in understanding why some species are aquatic and sister taxa on the same island are not, as is the case for cone, bugle, and burrito case types on Oahu and Maui.

Another example of this discordance in speciation patterns is revealed by comparing species diversity across the islands. Cone-cased species are aquatic on

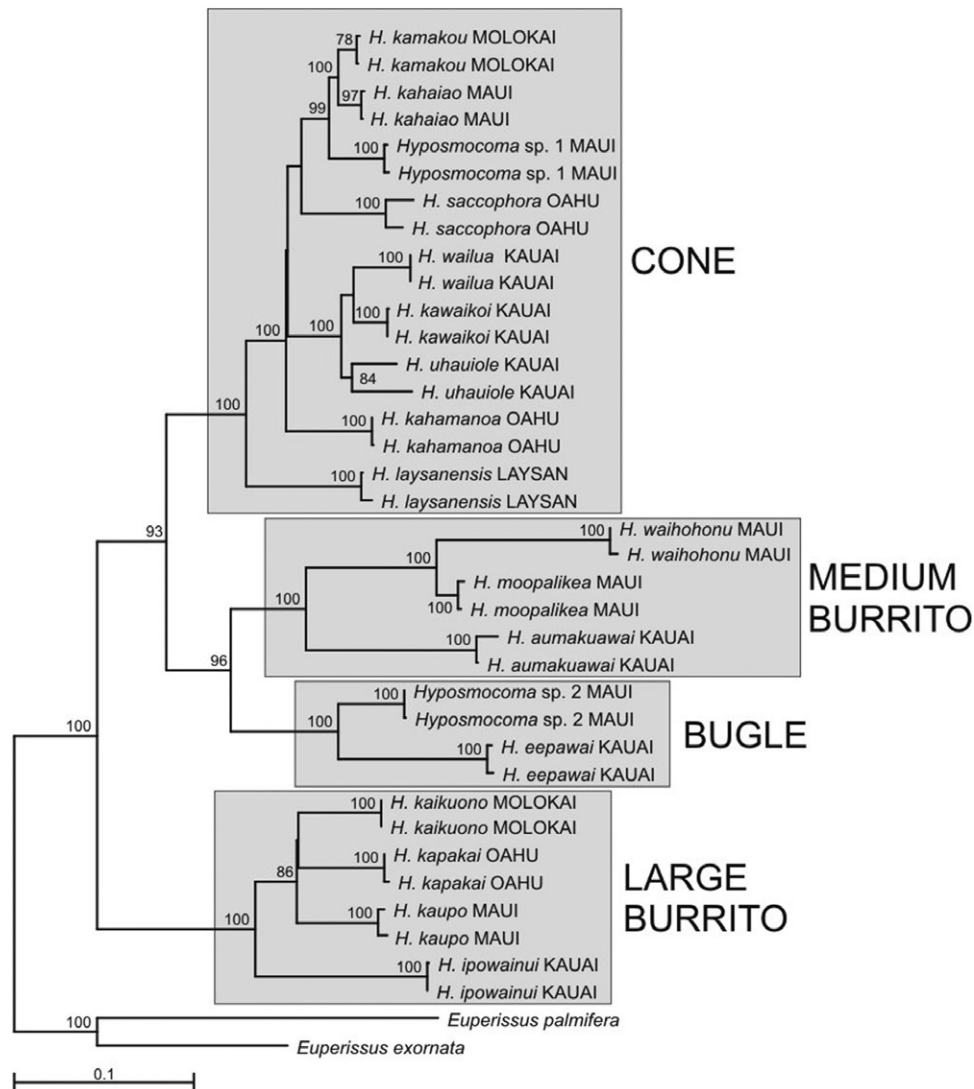


Figure 21. Maximum likelihood tree of *Hyposmocoma* species based on the combined analysis of three partial gene sequences: the mitochondrial gene *cytochrome oxidase subunit I* and, the nuclear genes *elongation factor 1 alpha* and *carbamoylphosphate synthetase*. The four monophyletic case lineages including the amphibious species described in the text are highlighted. Only bootstrap support values higher than 70% are given.

the older islands, but essentially absent in streams on the youngest volcanoes of east Maui and the island of Hawaii. In contrast, aquatic burritos are common and diverse across the entire island chain, including streams on east Maui where there are multiple species. Further adding to the complexity, only on Kauai does a single burrito species occur across an entire island; every other island has multiple species of burrito, occurring sympatrically.

Although each of the main Hawaiian Islands bears at least one aquatic case-bearing species (except the dry island of Lanai with no perennial streams), the island of Kauai has six species inhabiting its various streams and rivers. First, Kauai is the only island

where an aquatic burrito-case species occurs in all an island's streams and rivers. Second, Kauai is the only island where two cone-case *Hyposmocoma* species are sympatric, in the Wailua river (Fig. 22). Third, Kawaikoi stream, having its source in the Alaka'i swamp, contains four case-bearing aquatic *Hyposmocoma* species, each belonging to a different lineage. Such high diversity observed in only one stream is probably correlated with the fact that Kauai is the oldest high island and harbours one of the wettest places of earth (Giambelluca, Nullet & Schroeder, 1986). *Hyposmocoma* species from the older Northwestern Hawaiian Islands (Schmitz & Rubinoff, 2009), and the seashores of the main Hawaiian

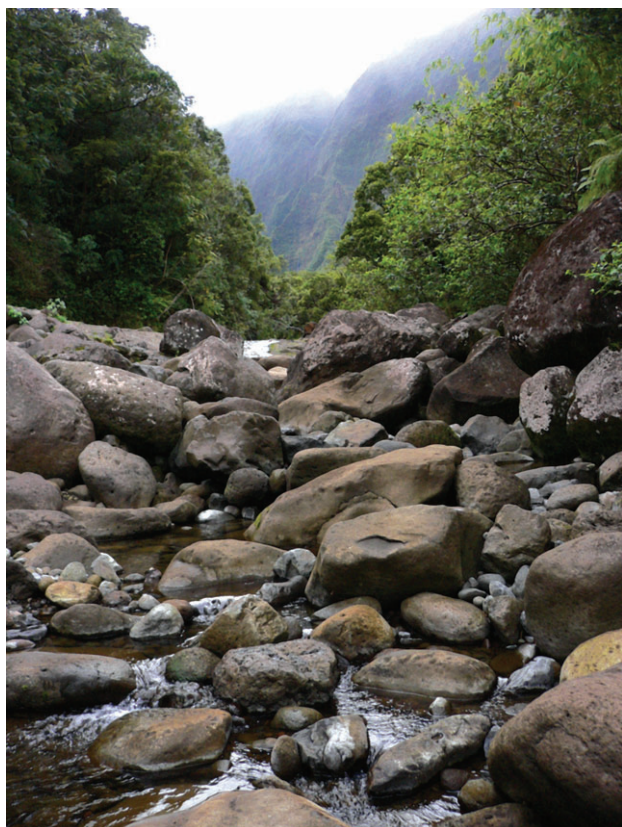


Figure 22. Typical habitat of aquatic *Hypsmocoma* species. The Wailua river on the eastern side of the island of Kauai shelters three different species from two different case types of aquatic case-bearing larvae: *Hypsmocoma ipowainui* sp. nov., *Hypsmocoma uhauiole* sp. nov., and *Hypsmocoma wailua* sp. nov.

Islands (Schmitz & Rubinoff, 2008), are strictly terrestrial, but some of these species belong to the same lineages as the aquatic species. This suggests that adaptation to an aquatic lifestyle has probably evolved repeatedly and independently (Rubinoff & Schmitz, 2010).

Biogeographically, the Hawaiian Islands may be best considered as a series of volcanoes, on islands, some of which are secondarily connected by lowlands. For example, the west Maui volcano, Pu'u Kukui, is significantly older and more eroded than the recently dormant volcano of east Maui, Haleakala (Price & Clague, 2002). Thus, organisms on west Maui may show a closer affiliation with the biota of the adjacent island of Molokai than with that of east Maui (Liebherr, 1997), as we also found in our phylogeny (Fig. 21). Similarly, the Waianae and Ko'olau mountain ranges of Oahu each represent separate eroding volcanoes. This may help to explain why there are different species of both cones (terrestrial vs. aquatic) and burrito (on Maui) on the two mountain ranges of

Oahu and Maui. As Kauai is even older, the current diversity of species may reflect ancient volcanic peaks that previously isolated lineages in a similar manner, essentially making the unusual diversity on Kauai the result not only of time, but also of vanished geology. For some reason aquatic bugle cases are restricted to Kauai, although terrestrial bugle cased species are known from Maui. This and the presence of various terrestrial cone species, one on east Maui (an undescribed species) one on west Oahu, *H. sacco-phora*, and three on the Northwestern Hawaiian Islands: *H. laysanensis*, *H. opuumaloo*, and *H. kolukiko* (Schmitz & Rubinoff, 2009), hint at the progression from terrestrial to aquatic species in each independent lineage.

None of the aquatic species discussed here occurs in highly modified habitats, and thus none are present in the lower reaches of their respective streams where human activity has changed the hydrological cycles, or destroyed the natural streambed. Each species, especially those endemic to single streams or drainages, particularly on Kauai (*H. eepawai*, *H. kawaikoi*, and *H. wailua*), is vulnerable to extinction because of past and on-going water diversions for human use. In many cases mountain streams run dry below such agricultural dikes. These *Hypsmocoma* caterpillars have yielded an important and novel view of insect evolution in an isolated archipelago, and the diverse genus to which they belong is likely to have much more to offer if its diversity can be adequately conserved. Moreover, as Hawaii lacks native members of most of the invertebrate groups typically used as bioindicators of water quality (Ephemeroptera, Megaloptera, Plecoptera, Trichoptera), aquatic *Hypsmocoma* species may have an important role to play in such assessments as water quality indicators.

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